Tools for managing threatened species:

improving the effectiveness of whio conservation

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Table of contents

Abstract

Conservation frequently requires immediate responses to prevent further declines of imperilled populations, often in the absence of detailed information. Consequently, population distribution patterns are often used to guide conservation decisions. However, distribution patterns may be misleading if threats have restricted species to low quality habitat. This issue means it is not always apparent where management efforts should be concentrated for maximum conservation gain. My aim was to improve the effectiveness of threatened species conservation by investigating this issue in whio (blue duck - *Hymenolaimus malacorhynchos*), a New Zealand riverine duck that has undergone serious declines. I used population and spatial modelling to answer three questions: (1) what are the threats to whio, (2) how can these threats be managed, and (3) managing which whio habitats will give the greatest conservation gain?

A spatial analysis of contemporary whio habitat using boosted regression trees revealed whio are only secure in 1 % of their historical range, with predation likely causing significantly greater range contraction (83 %) than habitat modification (29 %). In that analysis, I identified 39,000 km of occupiable whio habitat, providing extensive opportunities to expand their contemporary range through management. Intensive monitoring identified stoats (*Mustela erminea*) as the primary cause of whio population declines, with stoat predation severely reducing whio nest survival (10 % and 54 % in the absence and presence of stoat control, respectively). Population viability analyses indicated whio populations in the absence of stoat control were at high risk of extinction ($\lambda = 0.74$) but large-scale, low-intensity predator control was useful for short-term whio conservation. However, whio populations with stoat control still had a declining population growth rate ($\lambda = 0.95$) and further intervention may be required to prevent whio extinctions. Such management needs to target high quality habitat to ensure the greatest conservation value. Analyses of habitat quality revealed whio fitness was highest in warm, low gradient riv-

ers, although fitness gradients differed between North and South Islands. Comparisons of fitness relationships with spatial model predictions showed that South Island whio occurred more frequently in poorer habitat, indicating they may occupy a relict distribution.

Limited resources for conservation mean identifying effective management techniques is critical for species persistence. My modelling approach enabled the effectiveness of whio management to be assessed and areas of high quality habitat where such management should provide the greatest benefit to be identified. These tools are directly applicable to the conservation management of many threatened species by quickly informing managers in situations where distributions may not follow habitat quality.

Preface

Conservation management, like emergency medicine, involves making difficult decisions about the allocation of scarce resources wisely to preserve valuable life (Bottrill et al. 2008, 2009). Managers are frequently required to make immediate responses to prevent further declines of imperilled populations, often in the absence of detailed information (Grantham et al. 2009). Consequently, population distribution patterns are often used to guide conservation decisions. However, distribution patterns may be misleading if threats have restricted species to low quality habitat (van Horne 1983, Battin 2004). This issue means it is not always apparent where management efforts should be concentrated for maximum conservation gain. Conservation that targets inappropriate threats or undertakes management in low quality habitat may risk wasting limited resources or, in worst-case scenarios, result in continuing population declines despite management efforts (Crouse et al. 1987, Doak et al. 1994, Keedwell et al. 2002). Therefore, effective conservation requires clear identification of high quality habitat, where threatened species should respond most quickly to management (Sergio and Newton 2003), and the threats present within that habitat (Moilanen 2008, Briggs 2009). It is also vitally important to assess the effectiveness of management techniques through structured monitoring to ensure that conservation efforts actually lead to increases in population viability (Stem et al. 2005). Failure to do so may be costly, both from an economic standpoint and in terms of species persistence (Wakamiya and Roy 2009).

My aim was to improve the effectiveness of threatened species conservation by investigating these issues in whio (blue duck - *Hymenolaimus malacorhynchos*), a New Zealand riverine duck that has undergone serious declines. Whio have become the focus of intensive conservation management through large-scale, low-intensity predator control by the New Zealand Department of Conservation along rivers aimed at reducing predator densities within natural whio habitat (van Klink 2009). The long term goal of

the Whio Recovery Group is to ensure that key populations of whio are restored and self-sustaining in the wild throughout their natural range (van Klink 2009). However, prior to my research, little was known about the major predators of whio, the effectiveness of contemporary management techniques, and the characteristics of high quality whio habitat. Thus, there were few tools were available to guide management decisions for whio conservation.

In this thesis, I use population and spatial modelling to answer three questions: (1) what are the threats to whio, (2) how can these threats be managed, and (3) managing which whio habitats will give the greatest conservation gain? Although my analyses concentrate on improving whio conservation, my research tools could easily be applied to other threatened species. In Chapter One, I use species distribution modelling to quantify the relative influence of two potential threats, introduced predators and habitat modification, on the historic range contraction of whio by making predictions of their potential pre-human and contemporary distributions. This analysis addresses a fundamental question in extinction ecology and identifies areas of potential whio habitat that may provide opportunities for future conservation efforts. Chapter Two identifies the primary agent of decline in contemporary whio populations and looks at the impacts of current management actions on the demographics of a population in southern New Zealand. This work is extended using population viability analysis in Chapter Three to evaluate the effectiveness of management in ensuring long-term population viability. Chapter Four investigates the habitat-fitness relationships of nine whio populations over a broad geographic range to determine the characteristics of high quality whio habitat and identify areas where managers should get more value from conservation efforts. Chapter Five summarises and explores my overall findings, placing my research within the context of current ecological knowledge and develops a framework for effective conservation management. My modelling approach enables the effectiveness of whio management to be assessed and areas of high quality habitat where such management should provide the greatest benefit to be identified. These tools are directly applicable to the conservation

management of many threatened species by quickly informing managers in situations where distributions may not follow habitat quality.

This thesis has been structured as a series of stand alone scientific papers intended for publication. Such a format necessitates some repetition between chapters, but I consider it to be the most effective and efficient way to present my work. Each chapter is multi-authored, but the analysis and writing are largely my own, with the contributions of additional authors listed in individual chapter acknowledgements. Chapter Two was published in *Biological Conservation* in 2008 and is referred to as Whitehead et al. (2008) throughout the thesis, while Chapter Three is currently in press with *Austral Ecology* and is referred to as Whitehead et al. (in press). All other chapters are referenced by their chapter number. Figures and tables are numbered from the beginning within each chapter, while all references are provided at the end of the thesis to avoid repetition.

Chapter One

Predation vs. habitat modification: quantifying the drivers of global change

Abstract

Invasive species and habitat modification are linked to global species extinctions and declines, but their relative importance is uncertain, making management difficult in many situations. I used an advanced statistical technique (boosted regression trees) and almost three decades of range observations to quantify the relative impacts of these drivers of global change at the landscape-scale by making predictions of the pre-human and potential contemporary distributions of a threatened New Zealand duck. I reveal *Hymenolaimus malacorhynchos* have undergone catastrophic declines linked to mammalian predation and its interaction with habitat modification (range losses of 82 % and 29 %, respectively). My method of species distribution modelling highlights the importance of considering the synergistic effects of global change drivers in species declines and extinctions, and provides a powerful tool for conservation planning at landscape scales.

Introduction

Invasive species and habitat modification are two of the most important drivers of global extinctions and declines, particularly on oceanic islands (Gaston et al. 2003, Clavero and Garcia-Berthou 2005, Butchart 2008). Habitat modification and exotic mammalian predators have been labelled as the dominant independent drivers of avian extinctions (Gaston et al. 2003, Blackburn et al. 2004). However, the onset of these drivers is often highly correlated, with additive or synergistic effects likely (Gurevitch and Padilla 2004,

Didham et al. 2005a), For example, Didham et al (2005a, 2005b) argued that habitat modification is strongly correlated with both the introduction of mammalian predators and avian extinctions, making it difficult to disentangle the relative influence of these drivers of global change (Didham et al. 2005a, but see Trevino et al. 2007, Karels et al. 2008). These factors have led to considerable debate (Blackburn et al. 2004, Gurevitch and Padilla 2004, Didham et al. 2005a, Didham et al. 2005b, Duncan and Blackburn 2007, Trevino et al. 2007, Blackburn et al. 2008, Karels et al. 2008), with little resolution over the relative influence of predation and habitat modification. Distinguishing between these mechanisms of extinction and decline is important, both for understanding the influence of global change and for improving the focus of current management programmes. Recent advances in species distribution modelling and long-term, landscape-level data may provide a practical solution.

The development of methods to derive high resolution measures of habitat at the scale of landscapes, coupled with the availability of large databases containing long-term species range data, means it is now possible to use advanced statistical techniques, such as boosted regression trees (BRT; Friedman 2002), to predict potential distributions over vast areas (Elith et al. 2006). Such techniques also enable hindcasting or forecasting of potential distributions under known or predicted past and future environmental conditions (Hilbert and Ostendorf 2001, Balbontin et al. 2008, Waltari and Guralnick 2009). Distribution data are typically available for many threatened species that have undergone considerable range contractions due to localised extinctions, providing opportunities to investigate the relative impacts of potential extinction mechanisms (Ricciardi 2004, Elith and Leathwick 2007). Using threatened species to assess the impacts of extinction mechanisms will not only shed light on relative causes of past extinctions (Didham et al. 2005a), but also provide valuable information to guide current conservation management.

New Zealand's avifauna has been severely depleted since human colonisation, with habitat modification and introduced mammalian predators thought to be the primary drivers of extinction and decline for most species (Holdaway 1989). However, the relative

impacts of these mechanisms are unknown, making it difficult to prioritise and focus conservation management. I assess the relative impacts of introduced predators and the interaction between predators and habitat modification on the decline of a threatened New Zealand duck. *Hymenolaimus malacorhynchos* (whio, blue duck) is an endemic riverine duck that has declined in distribution and abundance due to habitat modification and predation by introduced mammalian predators (Kear 1972). Contemporary whio populations are sparsely distributed throughout New Zealand with small, fragmented populations in a wide range of largely unmodified habitats protected within conservation reserves (Figure 1; Collier et al. 1993). Despite habitat protection, whio continue to rapidly decline (Robertson et al. 2007). Their range contraction provides an opportunity to assess the relative influence of habitat modification and predation as drivers of global change.

Figure 1. The eclectic nature of habitats occupied by contemporary populations of whio in New Zealand suggests their range is not restricted by a lack of suitable habitat (Photos: A.Whitehead).

Methods

Whio distribution data

Whio distribution data were obtained from the New Zealand Department of Conservation's BioWeb database, which holds sighting records for native species throughout New Zealand. As most of the whio sightings were recorded prior to the widespread availability of geographic positioning systems (GPS), a 250 m buffer was applied to all data points and buffered sites that did not fall on a waterway were discarded. The resulting dataset contained 6,378 whio sightings between 1979 and 2006. Observations were widely distributed across New Zealand, occurring in habitats representative of the known range of whio.

Each record was intersected with the River Environments Classification (REC) geographic information system (GIS) database (Leathwick et al. 2008a). This is a network topology of New Zealand's rivers and streams, in which each segment describes the stream course between two adjacent confluences. Multiple records of whio from a segment were combined to give a single presence record, while multiple segments were often associated with a single presence record due to whio being present at stream confluences. In all, I identified 10,027 river segments where whio were present between 1979 and 2006. I sub-sampled this dataset, randomly partitioning off 1,000 records as training data for model development and keeping the remainder for independent evaluation.

My whio dataset did not contain information about whio absences from segments, so I utilised background data selected randomly from a geographically constrained area based on a kernel density plot of whio presences. Restricting the area for background data selection prevents artificial inflation of the test statistics, producing a more realistic measure of important environmental predictors (Chefaoui and Lobo 2008, Phillips et al. 2009, VanDerWal et al. 2009). I selected ten times more background points than whio presence points to ensure the background habitat was comprehensively described (Thuiller et al. 2004, Chefaoui and Lobo 2008, Phillips et al. 2009). However, background points were

down-weighted during modelling so that presence and background points had the same weight to avoid biases associated with extremely high numbers of absences (Dixon et al. 2005, Elith et al. 2006, Phillips et al. 2009). An additional 10,000 records were randomly selected from within the density kernel for independent evaluation of the model.

Environmental predictors

Whio are riverine birds, with environmental factors associated with water flow and terrestrial inputs likely to be important in structuring their distribution (Collier et al. 1993, Collier and Wakelin 1996, Sullivan et al. 2007). Therefore, I selected 16 biologically relevant environmental predictors from the REC that describe the river conditions at two spatial scales: local and upstream catchment. Descriptions of how these variables were derived are given in Table 1, with further details in Leathwick et al. (2008a). Whio are not restricted by downstream passage, so I did not consider the influence of downstream environmental conditions.

Statistical modelling

Boosted regression trees (BRT) are an advanced regression technique based on machine learning (Friedman 2002) and are being used increasingly to model the distributions of species (Elith et al. 2006). BRT are capable of dealing with non-linear relationships between variables and can assess high-order interactions, making them particularly suited for ecological data (Elith et al. 2008). BRT models are also robust to the effects of outliers and irrelevant predictors (Leathwick et al. 2006).

I used BRT to analyse the relationship between whio occurrence and the environment. All analyses were carried out in R (version 2.11, R Development Core Team 2005) using the 'gbm' library of Ridgeway (2004) and functions from Elith et al. (2008). The models were allowed to fit interactions, using a tree complexity of five and a learning rate of 0.05. I used ten-fold cross validation to determine the optimal number of trees for each model, giving the maximum predictive performance. After fitting an initial model, the

fitted functions of each environmental predictor were assessed for stability and biological functionality. I refitted the model, specifying the terms for several variables so that the fitted functions were constrained using monotonic relationships (*SegSumT* – negative monotone; *SegLowFlow* – negative monotone; *SegFlowStability* – positive monotone; *SegSlope* – negative monotone; *USRainDays* – positive monotone; *USSlope* – negative monotone; *USGlacier* – negative monotone). This procedure stabilised the functions and did not greatly reduce model performance. BRT models have a tendency to over-fit the

Table 1. Environmental parameters describing the riverine habitat of whio used in the boosted regression tree models. Parameters were derived from the River Environments Classification (REC) geographic information system.

Local scale predictors	**Whio mean & range**
SegSumT – summer air temperature (°C)	14.51 (6.50 to 18.70)
SegTSeas – winter air temperature (°C), normalised with respect to *SegSumT*, i.e. a $SegTSeas = \left(\left(\frac{W-\overline{W}}{\sigma_W}\right)-\left(\frac{S-\overline{S}}{\sigma_S}\right)\right)\times\sigma_S$ where W is the winter temperature for segment, $\overline{W}$ is the average winter temperature for all segments, σ_W is the standard deviation of winter temperature, S is the summer temperature, and so on.	0.41 (-2.46 to 3.32)
SegLowFlow – segment mean annual 7-day low flow ($m^3 s^{-1}$), fourth root transformed, i.e. $(\text{low flow} + 1)^{0.25}$	1.14 (1.00 to 3.12)
SegFlowStability – annual low flow/annual mean flow (ratio)	0.29 (0.01 to 0.59)
SegSlope – segment slope (°), square-root transformed	2.39 (1.00 to 6.85)
SegShade – riparian shade (%)	0.57 (0.00 to 0.80)
Landscape scale predictors	
USAvgT – average air temperature (°C), normalised with respect to *SegSumT*	-0.90 (-7.88 to 3.03)
USRainDays – days per year with rainfall greater than 25 mm	46.90 (4.00 to 127.59)
USSlope – average slope in the catchment (°)	26.04 (0.28 to 20.28)
USCalcium – average calcium concentration of underlying rocks, 1 = very low to 4 = very high	1.37 (0.00 to 4.00)
USHardness – average hardness of underlying rocks, 1 = very low to 5 = very high	3.59 (0.00 to 5.00)
USPhosphorus – average phosphorus concentration of underlying rocks, 1 = very low to 5 = very high	2.03 (0.00 to 5.00)
USLake – area of lake in catchment (%)	0.0006 (0.00 to 0.33)
USNative – area with indigenous vegetation (%)	0.94 (0.00 to 1.00)
USGlacier – area of glacier in catchment (%)	0.01 (0.00 to 0.87)
USPeat – area of peat in catchment (%)	0.0001 (0.00 to 0.15)

training data, so the performance of the model was assessed by making predictions at sites that were not used during model development. Two values were calculated for the model: the predictive deviance, and the discrimination as measured by the area under the receiver operator characteristic curve (AUC; Hanley and McNeil 1982).

I used the species-habitat relationships from the BRT model to make spatial predictions about the potential distribution of whio prior to human arrival in New Zealand, and their potential contemporary distribution if predators were absent. Spatial predictions were made in R using a script available in 'gbm' (Leathwick et al. 2006) and environmental data from the REC database. This procedure generated a relative index of the likelihood of whio occurrence across all New Zealand waterways. I considered values greater than the 90th percentile to indicate the likely presence of whio. Spatial predictions of the historical range of whio were made by replacing the contemporary values of *SegSumT*, *SegTSeas*, *SegShade* and *USNative* with values estimated for segments prior to the arrival of humans in New Zealand (Leathwick 2001). I calculated the length of potential whio habitat predicted under each scenario by summing the length of river predicted to contain whio. By comparing potential contemporary and pre-human distributions with the actual contemporary distribution, I estimated the relative impacts that predation, and the interaction between predation and habitat modification, have had in contracting the observed range of whio.

Table 2. Predictive performance of a boosted regression tree (BRT) model predicting whio occurrence.

	Cross-validation* (11,000 sites)	**Evaluation data** (18,000 sites)
Percentage deviance explained	61.8 (0.8)	54.2
Area under receiver operator characteristic curve	0.948 (0.003)	0.956

*1000 presence sites with 10000 randomly selected background sites downweighted to equal the presence sites. Mean and SE estimated during model building.

Results

My models had excellent discriminatory power (Table 2) and showed the contemporary distribution of whio was characterised by a combination of local environmental conditions and factors operating in the upstream catchment (Figure 2; Table 3a). Whio were most likely to occur in small, stable rivers, with upstream catchments characterised by a high proportion of native vegetation, high rainfall and cold temperatures (Figure 2a). I also identified a strong interaction between *USAvgT* and *SegTSeas*, with the probability of whio occurrence increasing in segments with cold upstream catchments and average

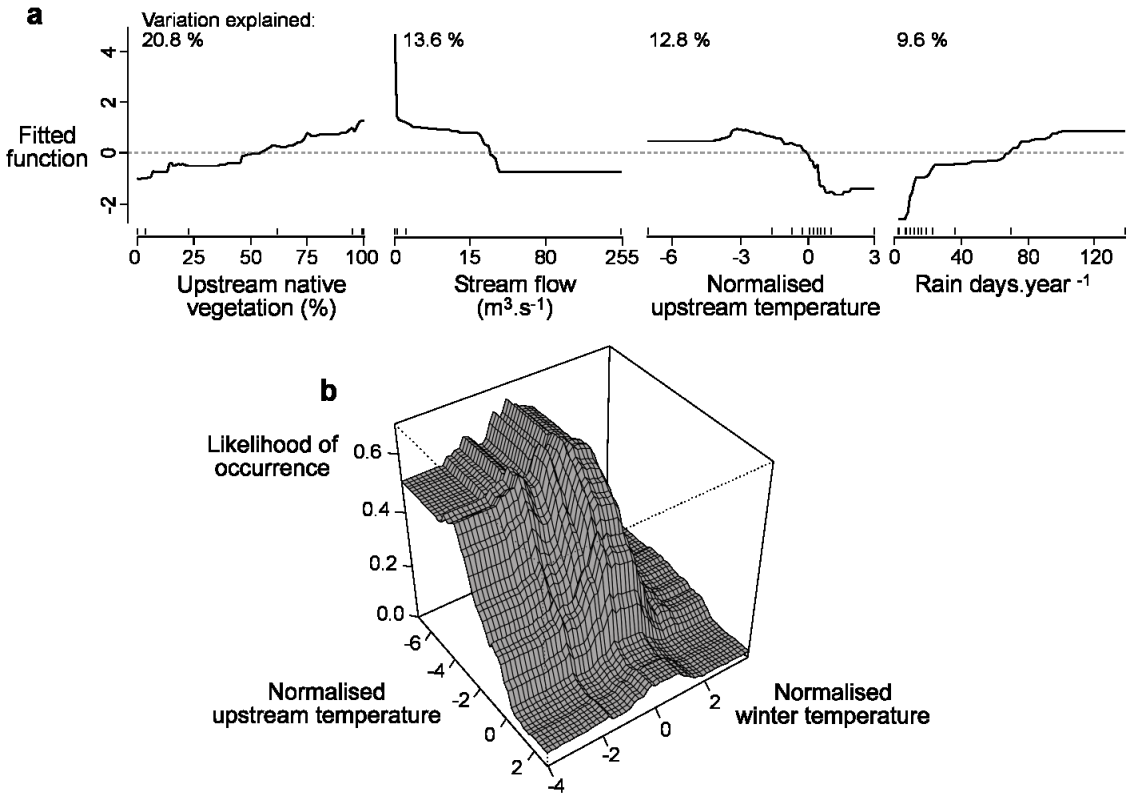

Figure 2. Key relationships between habitat and the likelihood of whio occurrence, showing (a) the four most important predictors in a boosted regression tree (BRT) model. The dotted line represents the threshold above which whio occurrence is likely. Decile ticks above the x-axis of plots show the distribution of data for each variable. (b) Three-dimensional partial dependence plot for the strongest interaction in the BRT model of whio occurrence. Upstream and winter temperatures are normalised relative to the local summer air temperature. To produce the plots variables except those graphed were held at their means.

winter temperatures relative to local summer temperatures (Figure 2b). Other significant interactions included relationships between *SegSlope* and *SegLowFlow*, and *USPhosphorus* and *USAvgT* (Table 3b). My results concur with those from earlier research, which indicate that climatic and instream hydraulic conditions have an important influence on the distribution of whio (Collier et al. 1993).

I predicted 54,000 linear km of riverine habitat suitable for whio prior to human arrival in New Zealand. In comparison, there is approximately 39,000 km of suitable habitat available under contemporary habitat conditions in the absence of predators (Figure 3). A large proportion of the predicted pre-human range, particularly in the North

Table 3. Summary of the most important environmental predictor variables for a boosted regression tree (BRT) model of whio occurrence. (a) Relative contribution of the ten most important predictor variables. (b) The top five pairwise interactions between predictor variables. The interaction strength indicates the relative degree of departure from a purely additive effect, with a value of zero indicating that no interaction is present. For explanations of variables and their units see Table 1.

a) Relative contribution of predictor variables	
Predictor	**Relative contribution (%)**
USNative	20.79
SegLowFlow	13.64
USAvgT	12.76
USRainDays	9.61
SegShade	8.50
SegFlowStability	7.58
SegSlope	6.25
SegTSeas	5.89
SegSumT	4.52
USPhosphorus	4.30
b) Pairwise interactions between predictor variables	
Predictors	**Interaction strength**
USAvgT & *SegTSeas*	92.20
SegSlope & *SegLowFlow*	35.88
USPhosphorus & *USAvgT*	32.84
USNative & *SegTSeas*	28.96
USAvgT & *SegLowFlow*	25.13

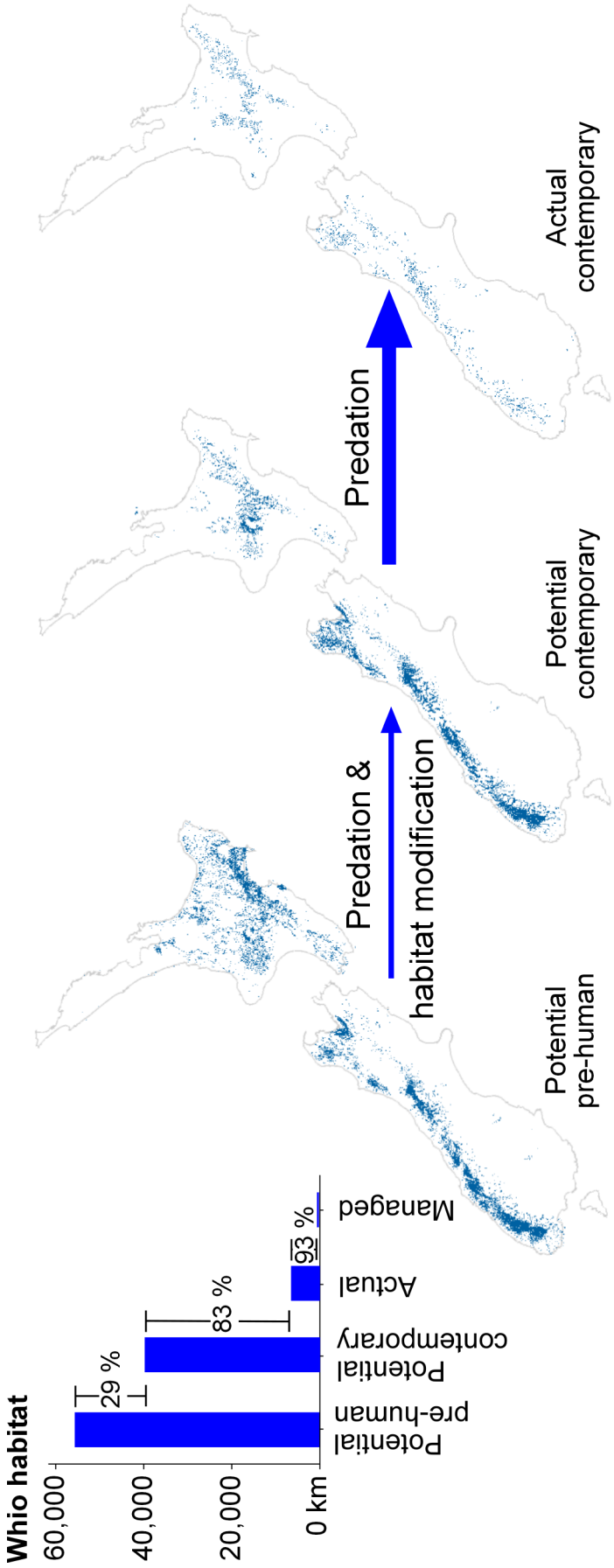

Figure 3. The relative impacts of predation and habitat modification on the distribution of whio predicted using a boosted regression tree (BRT) model. Maps show the predicted distribution of whio prior to human arrival in New Zealand, in contemporary habitat with the exclusion of predators, and the actual current distribution. Labelled arrows represent the likely cause of the predicted range contraction, while the amount of suitable whio habitat lost due to habitat modification and exclusion by predators is shown in the graph.

Island, occurred in areas subsequently cleared of native vegetation after human arrival. Thus, I estimated that whio suffered a 29 % range contraction brought about by the interaction between habitat modification and predation. Contemporary whio populations only occupy about 7,000 km of riverine habitat. Habitat within the predicted potential contemporary range is largely unmodified, meaning that effects of predators are the likely cause of the additional 83 % contraction in their range. The range contraction of whio due to predation has resulted in a highly fragmented contemporary distribution, with extant populations confined to small isolated areas within the matrix of unoccupied potential habitat. Only 600 km of their current range (or 1 % of their likely pre-human range) is actively managed (Whio Recovery Group, *pers. comm.*).

Discussion

By revealing the magnitude of population declines and partitioning the mechanisms, my analyses identify predation as the major driver of range contraction. They also provide guidance to managers by highlighting the large amount of potential habitat that whio could occupy if the effects of predation can be mitigated. Controlling stoats is possible, with large-scale, low-intensity predator control significantly increasing whio productivity (Whitehead et al. 2008). Conservation managers have considerable scope to expand whio populations into new areas in this way and can prioritise sites based on my predictions of likely whio occurrence.

Explicitly considering the synergies between drivers of global change is vital for understanding past declines and developing effective conservation management. Introduced predators have long been recognised as a contributing factor in the decline of avian species, particularly on oceanic islands (Gaston et al. 2003, Clavero and Garcia-Berthou 2005, Butchart 2008), but their relative influence compared to other drivers of global change was unclear (Blackburn et al. 2004, Gurevitch and Padilla 2004, Didham et al. 2005a, Didham et al. 2005b, Duncan and Blackburn 2007, Trevino et al. 2007, Black-

burn et al. 2008, Karels et al. 2008). My approach provides a way of quantifying the relative effects of multiple mechanisms of species decline and extinction by using new landscape-scale modelling techniques to analyse readily available information about species distributions. I have shown predation by introduced mammals to be the mechanism driving whio declines. Whio, like many avian species on oceanic islands, evolved in the absence of mammals, so have a range of behavioural traits, such as ground-nesting, that make them vulnerable to introduced mammalian predators. My analysis shows that this naivety to novel predators led to a considerable loss of habitat, with rapid declines still evident today (Whitehead et al. 2008).

However, my analysis also highlights likely synergistic interactions between predation and habitat modification. New Zealand suffered severe habitat modification after human colonisation, losing two-thirds of its native forest cover by the mid 20th century (Hall and McGlone 2006). However, this period of wide-spread deforestation is highly correlated with the introduction and establishment of mammalian predators (King 2005). Therefore, it is difficult to establish the exact form of the interaction between these two drivers of global change, but habitat modification likely played a role in the early declines and extinctions of island avifauna, with contemporary populations rarely found in areas dominated by exotic vegetation. I cannot rule out the contribution of other factors, such as demographic stochasticity, disease, and genetic and Allee effects, to population declines but it is most likely they only compounded the effects of predation rather than impacting populations directly (Duncan and Blackburn 2007). Introduced predators are recognised as the greatest threats to contemporary island avifauna (Blackburn et al. 2004) and my findings suggest that they were probably the most influential factor in avian extinctions on oceanic islands.

The increasing vulnerability of species to global change, coupled with a limited resource pool for conservation, means that effective conservation management is critical for species persistence. The growing availability of long-term observational datasets and geographic information systems containing large-scale environmental data makes it

possible for managers to apply my approach to a wide range of threatened species. BRT models provide a powerful tool for modelling species distributions to evaluate species-habitat relationships and make predictions about potential distributions. By using this approach to make comparisons of predicted potential distributions under different habitat conditions, managers can rapidly assess the relative impacts of potential threats, as well as identify habitats where conservation efforts could be targeted outside the current range. Such techniques will develop understanding of the global change mechanisms that drive species declines and help us to improve the focus of management towards appropriate threats, particularly in these times of rapid anthropogenic change.

Acknowledgements

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Chapter Two

Large-scale predator control improves the productivity of a rare New Zealand riverine duck

Abstract

Declines in avian populations are often attributed to the presence of introduced predators but conservation managers frequently lack good information about the effectiveness of potential predator control regimes for protecting threatened species. Whio (*Hymenolaimus malacorhynchos)* are a threatened New Zealand waterfowl that has been declining in both distribution and abundance. I conducted a six-year study using a paired-catchment experiment in New Zealand *Nothofagus* forest as part of an adaptive management programme to assess whether whio populations responded positively to stoat (*Mustela erminea*) control. Video monitoring identified stoats as the primary nest predator. Large-scale, low-intensity stoat control (10 traps per linear km) significantly reduced the stoat abundance index in the presence of stoat control. As a result, whio nest survival and productivity, the number of fledglings produced per pair, increased significantly in the presence of stoat control compared to sites where stoat control was absent. However, adult survival rates and the number of pairs did not change significantly between treatments. These findings identify stoats as the primary agent of decline for whio in this *Nothofagus* forest system, and show that large-scale, low-intensity stoat control is sufficient to improve the productivity of whio populations. Overall, the study demonstrates the value of an adaptive management approach whereby management techniques can be evaluated to ensure that the primary agent of decline is clearly identified and that predator densities are kept sufficiently low.

Introduction

Population declines of many species globally have been attributed to predation by introduced species (Blackburn et al. 2004). These trends have been pronounced on oceanic islands, where species have often evolved in the absence of mammalian predator (Courchamp et al. 2003). As a result, island species typically have behavioural and life-history strategies, such as flightlessness, ground-nesting and low fecundity, that make them vulnerable to predation by introduced mammals (Courchamp et al. 2003, Isaksson et al. 2007). For example, in New Zealand introduced mammalian predators such as stoats (*Mustela erminea*) have led to dramatic declines in a number of bird species mal-adapted to ground-based predators (Moors 1983, O'Donnell 1996). Therefore, threatened species management on islands is frequently reliant on the control or eradication of introduced mammalian predators. Managers are often required to make an immediate response to prevent further declines of already reduced populations, even in the absence of detailed information about the situation (McArdle 1996). This can sometimes lead to inappropriate management decisions and a waste of resources (Côté and Sutherland 1997, Keedwell et al. 2002). An adaptive management approach to conservation, where the current needs of management are balanced with the need to learn more about the system being managed, can be helpful (McLain and Lee 1996, Innes et al. 1999, Armstrong et al. 2007). Adaptive management works on the premise that management decisions can be effectively altered based on the outcomes of multiple hypothesis testing, despite an imperfect understanding of the system (McLain and Lee 1996, McCarthy and Possingham 2007). Such an approach can provide vital information regarding potential agents of decline and their impacts on population demographics, while simultaneously addressing the current needs of the system and monitoring the effectiveness of management tools (Innes et al. 1999, Stem et al. 2005, Armstrong et al. 2007, McCarthy and Possingham 2007).

Predator control for conservation purposes ranges in intensity from complete eradication to low-intensity, seasonally-targeted control aimed at reducing predator numbers

during periods of high prey vulnerability (Côté and Sutherland 1997, Courchamp et al. 2003). Eradication, when successful, is the most effective method of predator control, but it may be impractical over large areas or with certain suites of predators (Courchamp et al. 2003). Therefore, the development of reliable low-cost control techniques to reduce predator densities is paramount for many conservation programmes. This is particularly important for threatened species that cannot be translocated to predator-free sites, such as offshore islands, due to specific habitat requirements. Current control measures around the world include both lethal (i.e. kill traps, toxicants, hunting) and non-lethal methods (i.e. live traps, fences) but it is difficult to predict which methods are sufficient for successful species recovery, with results often variable within and between studies (Côté and Sutherland 1997, Courchamp et al. 2003). This is particularly true for waterfowl management, where a wide range of predator control techniques, ranging in intensity, are used globally with variable success (Lokemoen and Woodward 1993, Beauchamp et al. 1996, Opermanis et al. 2001, Nordstrom et al. 2002, Kauhala 2004).

In New Zealand, the endemic riverine whio or blue duck (*Hymenolaimus malacorhynchos*) has become the focus of intensive conservation management through large-scale, low-intensity predator control along river corridors aimed at reducing predator densities within natural whio habitat. Classified as *endangered* and *nationally endangered* by the IUCN and New Zealand Department of Conservation, respectively (Hitchmough et al. 2007, IUCN 2007), whio have declined in both distribution and abundance and they are now restricted to fragmented populations, mostly in headwater rivers of the central North Island and western South Island (Chapter One, Robertson et al. 2007a). These declines have been attributed to predation by introduced mammals and habitat modification through deforestation and flow regulation (Chapter One, King et al. 2000, Young 2006).

Whio exhibit a range of behavioural traits which may make them vulnerable to introduced mammalian predators now present in New Zealand. They are ground-nesters, often nesting under overhanging vegetation or in holes in the riverbank (Kear 1972). Only female whio are involved with incubation and the incubation period can last for up

to 35 days (Williams 1991), placing both the eggs and adult females at risk of predation for an extended period of time. Ducklings typically leave the nest and begin feeding on the river within 48 hours of hatching (Williams 1991). Low productivity, or low numbers of fledglings produced per pair, and male-biased sex ratios, have been observed in almost all studies of whio populations in untrapped catchments (van Klink 2009), implicating predation of nests and adult females as a cause of whio population declines. Whio are restricted to mainland riverine habitats where the eradication of mammalian predators is not feasible using current techniques. Therefore, current management for whio is dominated by lethal predator control regimes aimed at reducing the density of stoats (van Klink 2009). Stoats are known to prey on many New Zealand bird species (Moors 1983, King 2005) but it is unclear if they are an important agent of decline for whio or if large-scale, low-intensity stoat control is sufficient to reverse the observed decline in whio populations. In addition, it is unknown if other introduced mammalian species present in the area, such as rats (*Rattus norvegicus* and *R. rattus*) or possums (*Trichosurus vulpecula*), are also agents of decline for whio.

In 2000, following a report of serious declines in whio numbers in Fiordland National Park (Torr and Coates 1999), an adaptive management approach to whio conservation was proposed for two river catchments. It was hoped this would allow managers to protect the remaining birds, while simultaneously providing reliable information about threats to whio and the effectiveness of large-scale, low-intensity stoat control. I report on the outcome of that management including my assessment of the primary cause of current declines for whio and an examination of the influence of stoat control on whio productivity and survival. I also discuss whether the establishment of large-scale, low-intensity stoat control is sufficient to enable the recovery of whio populations.

Methods

Study area and design

Experimental control of stoats was carried out over a six-year period (2000-2006) using a paired-catchment design in Fiordland National Park, New Zealand (midpoint 44°S, 167°E, Figure 1). For the first three years of the study, stoats were controlled along 33.5 km of river in the Clinton valley, while the neighbouring Arthur valley was left unmanipulated. Stoat control (27.5 km) was established in the Arthur valley in April 2003 and monitoring continued in both valleys for an additional three years. The Cleddau catchment was also included in the study in October 2003 after stoat control (27 km) was established in the area through a community-driven initiative.

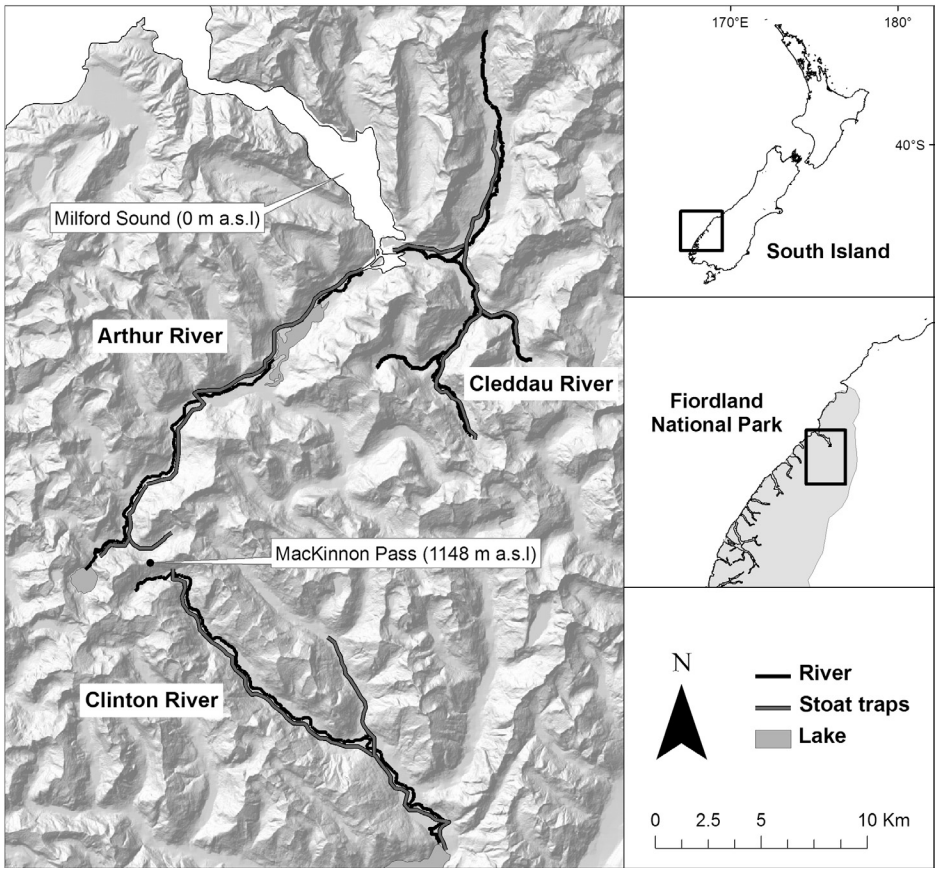

Figure 1. Rivers adjacent to the Milford Track in Fiordland National Park, New Zealand, where whio were monitored and stoat trapping was undertaken between 2000 and 2006. Milford Sound (0 m a.s.l) and MacKinnon Pass (1148 m a.s.l) are indicated to show the steep topography of the study area.

All three rivers are located in steep-sided glacial valleys (Figure 2) and range in altitude from 0 – 700 m above sea level. The valleys are dominated by silver beech (*Nothofagus menziesii*) forest, although red beech (*N. fusca*) is present in the lower reaches of the Clinton valley. The lower reaches of the Arthur and Cleddau valleys also contain some podocarp tree species.

Figure 2. Characteristic habitat of whio in the Clinton valley, Fiordland National Park. MacKinnon Pass (1148 m a.s.l) which separates the Clinton and Arthur valleys is shown in the distance. Inset. Female whio (*Hymenolaimus malacorhynchos*) with duckling.

New Zealand beech forest is characterised by irregular autumn masting events, when high quantities of seed are produced every three to five years (Wardle 1984) and more frequently in some rare cases. High quantities of seed lead to an increase in the numbers of introduced rodents (*Mus musculus, Rattus exulans*, *R. norvegicus* and *R. rattus*), followed by high densities of stoats during the following summer (King 1983). As a result, increased rates of mammalian predation have been noted for a wide range of native New Zealand species during these periods (Murphy and Dowding 1995, White and King 2006). Beech mast events occurred in the study area in 1999, 2000 and 2006.

Stoat control and monitoring

Stoats were controlled by kill-trapping, with wooden tunnels containing two Mark IV Fenn traps (King and Edgar 1977) set at 200 m intervals along existing walking tracks or roads along one side of each river. Tunnels were baited with a single hen's egg and a piece of meat between the traps, and were checked and rebaited approximately monthly. This intensity of predator control is low compared to that typically used overseas for waterfowl management (e.g. Sargeant et al. 1995, Beauchamp et al. 1996, Garrettson and Rohwer 2001, Nordstrom et al. 2002, Kauhala 2004). A standardised monthly capture rate was calculated per tunnel in the Clinton and Arthur valleys. An index of stoat abundance was also measured in the Clinton and Arthur valleys using footprint tracking tunnel lines (King and Edgar 1977). There were three tunnel lines in each catchment, each line consisting of 25 open-ended corrugated plastic tunnels spaced 25 m apart. Each tunnel was baited with meat on a central sponge soaked in red food dye placed between two papers that collected animal footprints. Tracking tunnels were placed out three times a year (early spring, mid-summer and early autumn) for one night. The average proportion of tracking tunnels in each line that contained stoat footprints was used to calculate an index of abundance (Innes et al. 1999). To assess the impact of control on stoat abundance indices, the tracking tunnel data were divided into two time periods; the first three years when the Clinton valley was trapped and the Arthur valley was untrapped, and the last three

years when both the Clinton and Arthur valleys were trapped. I used repeated-measures ANOVA to test the effects of sampling period and catchment on the abundance index of stoats with season as the repeated measure. Data were arc-sine square root transformed to meet the normality and homoscedascity assumptions of ANOVA.

Whio productivity and survival

All whio within the study area were banded and adult females fitted with 16 g radio transmitters using an external flying bird backpack harness. Transmitters were changed annually where possible, with an expected battery life of 18 months using a 12-hour duty cycle. At the beginning of each breeding season, adult females were located at least weekly in the Clinton and Arthur valleys using a handheld Yagi aerial (Sirtrack) and Telonics TR4 receiver (Telonics, Inc., Arizona, USA) to establish when nesting commenced. Nests were located on foot using radiotelemetry, and infrared cameras were set up on accessible nests to monitor nest fate and cause of nest failure. Nests were also inspected if a female was not present during a visit. Monitoring for nests in the Cleddau valley was less intensive; whio pairs were checked fortnightly and no video monitoring was undertaken. Nests were considered successful if at least one egg hatched. Nest survival (the proportion of nests surviving the 35 days from clutch initiation to hatching) was calculated for each treatment in program Mark 5.1 (Cooch and White 2006), with valley and year included as covariates.

Once ducklings were observed on the river, family groups were monitored regularly until fledging. Just prior to fledging, ducklings were banded with a colour cohort band (distinct for each of the three catchments) and a stainless steel number band. During the 2003/2004 and 2004/2005 breeding seasons, fledglings were also fitted with radio-transmitters.

Sightings of whio were recorded throughout the year during routine ground-based monitoring. Comprehensive surveys of each river were conducted in December and March each year to count birds and to detect and band new birds. The initial population

of whio in each catchment was assessed for an unbalanced sex ratio using a binomial test. Aerial radiotracking by helicopter using a custom built aerial was used to assess juvenile dispersal into neighbouring catchments. Whio are territorial, defending up to 2 km of river year round (Eldridge 1986), and sighting records were used to delineate pair territories. All transmitters were fitted with a mortality switch and attempts were made to locate dead birds as soon as possible. I used Fisher's exact test to evaluate differences in the rate of stoat predation between the management treatments.

Sighting and banding records were used to calculate apparent survival rates in program Mark 5.1 (White and Burnham 1999), using a Cormack-Jolly-Seber model based on live recaptures in an open population (Lebreton et al. 1992). Data within a summer monitoring period were pooled into one capture occasion, with capture histories constructed for six occasions for the years 2000-2005. I tested hypotheses that survival differed by catchment, sex, age (juvenile and adult) and management treatment using a set of candidate models created with the sin link for interactive models and the design matrix with the logit function for additive models (Cooch and White 2006). The most parsimonious model was selected using the quasi Akaike's Information Criterion ($QAIC_c$), corrected for over-dispersion using the ĉ adjustment (Cooch and White 2006).

Results

Stoat control and monitoring

The mean annual stoat abundance index ranged from 0 to 95 % of tunnels tracked over the six-year study period (Figure 3a). There was a significant interaction between sampling period and treatment ($F_{1, 24} = 136$, $p < 0.01$), with a high abundance of stoats in the untrapped Arthur valley in period one and low stoat abundances in the trapped catchments of both periods.

A total of 1,056 stoats were caught in the Clinton and Arthur valleys during the study period. The highest stoat captures in both valleys occurred during the first year of

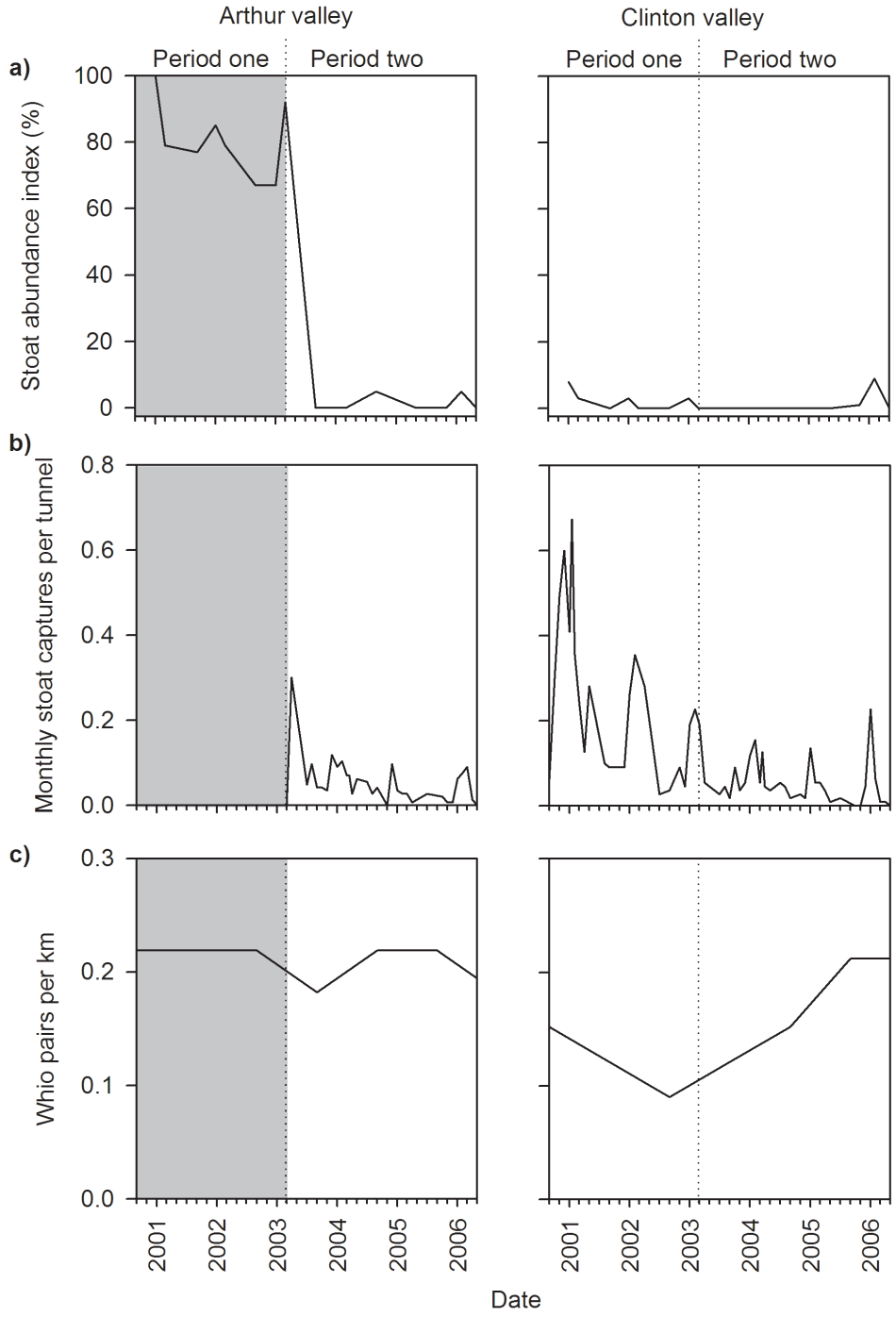

Figure 3. Stoat abundance index (a), capture rates (b) and whio pair densities (c) in the Arthur and Clinton valleys between 2000 and 2006. The stoat abundance index reflects the average percentage of tracking tunnels recording stoat footprints. During the first three years of the study (period one) stoat trapping was absent in the Arthur valley (shaded in gray) but present in the Clinton valley. Stoat trapping was present in all three valleys in period two. The Cleddau valley was not monitored for stoats or whio in period one and no reliable stoat abundance index or capture data were available for period two. Whio pair densities were recorded annually in September at the beginning of the breeding season.

control (Figure 3b), although seasonal peaks in stoat captures occurred consistently in late summer due to high numbers of juveniles. A high number of stoats were captured in the Clinton valley during the 2000/2001 and 2001/2002 summers, coinciding with expected peaks in food availability due to the beech mast events in the preceding years.

Whio productivity and survival

A total of 115 whio were banded in the Clinton, Arthur, and Cleddau valleys over the six-year study, with 57 known to be alive at the end of the study. The initial sex ratio of whio in the Clinton valley was heavily skewed towards males (3.2:1, $p = 0.01$), although no such bias was noted in the other two valleys (Arthur valley – 1:1, $p = 0.23$; Cleddau valley – 0.75:1, $p = 0.27$). The number of pairs present in the Arthur valley remained relatively constant throughout the study period, regardless of the presence or absence of stoat control (Figure 3c). In comparison, there was an initial decline in the number of pairs present in the trapped Clinton valley, followed by a steady increase from the 2003/2004 season onwards. Pair composition changed quite frequently in some parts of the study area, but the number and location of occupied territories remained relatively constant. The mean (± se) whio territory length was 1.7 ± 0.1 km.

Fifty nesting attempts were observed over the six-year study period, with 11 nests in the absence of stoat control compared to 41 nests with stoat control. However, there was no significant difference in the annual mean number of nests produced per pair between treatments ($t_{17} = 0.48$, $p = 0.64$; Table 1). Nests contained an average of 4.3 ± 0.2 eggs (range 2 - 6) with no infertile eggs found in any of the monitored nests. Overall appar-

Table 1. Mean (± se) annual productivity of whio measured in terms of nesting attempts, ducklings hatched and fledglings produced per pair in catchments with and without stoat control.

Treatment	Pair-Years	Nests	Ducklings	Fledglings
No stoat control	18	0.67 ± 0.17	0.22 ± 0.22	0
Stoat control	60	0.53 ± 0.07	1.17 ± 0.28	0.80 ± 0.24

ent nest survival differed significantly between the treatments (Figure 4), with 10 ± 1.9 % of nests hatching at least one duckling in the absence of stoat control compared to 54 ± 0.5 % of nests with stoat control. In addition, stoat control led to a significant increase in the mean annual number of ducklings hatched per pair ($t_{17} = 2.10$, $p = 0.05$; Table 1).

Predators could be clearly recognised on the nest camera video footage. Stoats were the primary nest predator, preying on both the eggs and the incubating female (Figure 4). Stoat predation accounted for 50 % of nest failures in the absence of stoat control, compared to 25 % with stoat control. Other nest predators included two native birds, weka (*Gallirallus australis*) and kea (*Nestor notabilis*), causing 11 % and 4 % of nest failures, respectively. Introduced possums and rats visited nests but none of the observed

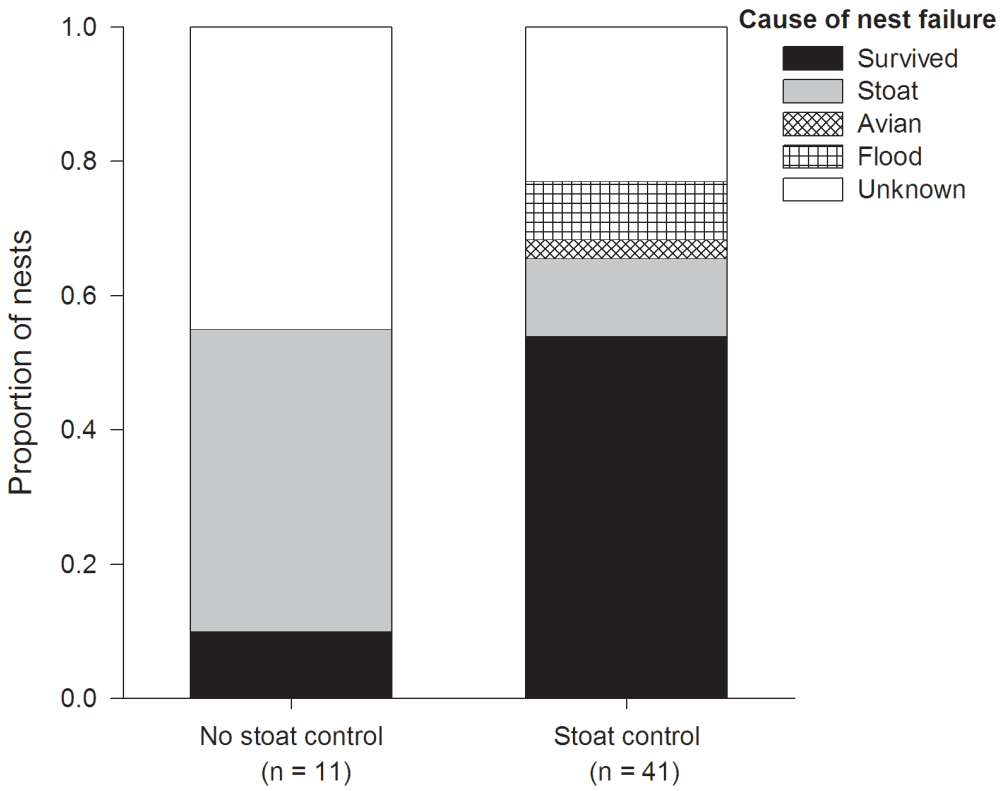

Figure 4. Whio nesting success and the causes of nest failure in response to stoat control. Nest survival rates were determined using the nest survival model in program Mark, while the cause of nest failure was identified using infra-red video monitoring and visual assessment of nest remains. The number of nests monitored under each treatment between 2000 and 2006 is given in parentheses.

visitations resulted in predation. Floods, where the nest was inundated, also led to nest failure on two occasions.

The mean number of fledglings produced per pair was significantly higher with stoat control ($t_{17} = 2.14$, $p = 0.05$; Table 1). No ducklings survived to fledge in the absence of stoat control; the four ducklings that hatched in the untrapped site, as well as the adult female, were killed by a stoat within three days of hatching. In comparison, 65 % of ducklings fledged with stoat control, producing 0.8 ± 0.24 fledglings per pair per annum. Over all study sites no ducklings fledged when the mean stoat tracking rate was greater than 5 % (Figure 5). Small ducklings frequently disappeared at times of high water flow suggesting that flood events may also contribute to duckling mortality.

Fifty-one juvenile whio were banded within stoat control sites during the six-year study period. Juvenile dispersal differed between sexes as males moved significantly further from their natal territory ($t_{11} = 2.03$, $p = 0.04$). Eighty-seven percent of females remained in their natal catchment, moving an average of 3.84 ± 0.60 km. In comparison, only 40 % of juvenile males remained in their natal catchment, with a mean dispersal distance of 8.77 ± 2.05 km. The greatest juvenile dispersal movement was made by a male moving approximately 24 km.

Table 2. The top five candidate models describing factors affecting survival (ϕ) and recapture probability (p) of whio using program MARK. AICc values were adjusted for ĉ of 1.25.

Model	**QAICc**	**ΔQAICc**	***w***	**n.p.**	**Qdev**
ϕ(age) p(constant)	179.55	0.00	0.23	3	84.63
ϕ(age + treatment) p(constant)	179.59	0.04	0.22	4	82.55
ϕ(catchment + age) p(constant)	180.19	0.64	0.12	4	83.15
ϕ(age + sex) p(constant)	181.46	1.91	0.09	4	84.42
ϕ(treatment) p(constant)	181.54	1.99	0.08	3	86.61

Quasi Akaike's information criterion (QAICc), differences in QAIC (ΔQAICc), Akaike's weight (*w*), number of parameters (n.p.) and deviance (Qdev).

The most parsimonious model (Table 2) indicated that survival varied by age, with juveniles displaying a lower survival rate than adults. There was also some evidence that the management treatment had an influence on whio survival, as shown by the small ΔQAICc values between models 1 and 2 and the insignificant likelihood ratio test (χ^2 = 2.08, d.f. = 1, p = 0.15). Catchment and sex also featured in the top five models and may influence whio survival. Therefore, I used model averaging (Cooch and White 2006) to account for the weightings of each model. The mean apparent survival for adults appeared to be higher in the absence of stoat control (female – 0.80 ± 0.10; male – 0.82 ± 0.09) compared to stoat control sites (female – 0.67 ± 0.07; male – 0.72 ± 0.07). Mean juvenile whio survival in the presence of stoat control varied between 0.48 ± 0.14 and 0.51 ± 0.14 for males and females respectively. No juvenile whio were present in the absence of stoat control.

Stoat predation on adult females was significantly lower in the presence of stoat control (Figure 6; Fisher's exact test, p = 0.02), with 25 % of adult female mortality

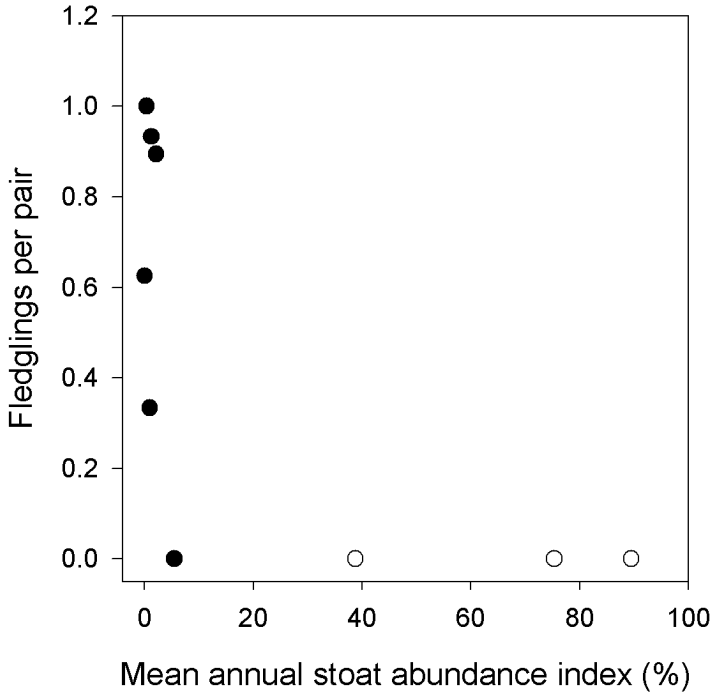

Figure 5. Number of fledglings produced per pair plotted against mean annual stoat abundance index for all catchments monitored during the study. Black and white symbols indicate data from sites with and without stoat control, respectively.

caused by stoats in the stoat control sites, compared to 100 % in the absence of stoat control. Other causes of mortality included bacterial infections (17 %) and predation by native falcons (*Falco novaeseelandiae*; 17 %). The remains of dead juveniles with transmitters were typically recovered in poor condition, although predation appears to be a contributing factor to juvenile mortality; at least one was killed by a stoat. The remains of another three juveniles suggested they had been preyed upon but it was not possible to identify the predator. An additional two juveniles were killed by avalanches during the

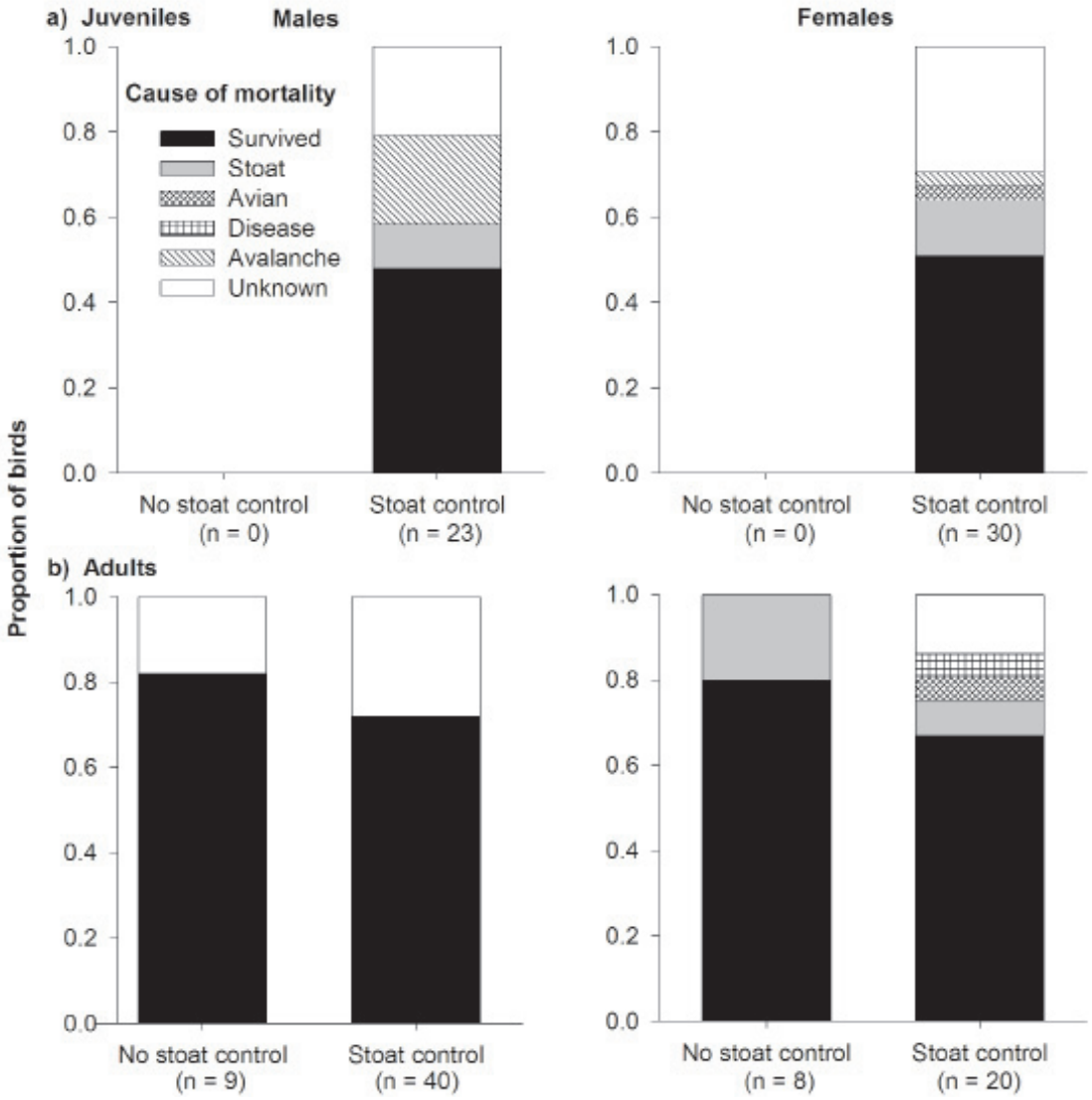

Figure 6. The apparent survival rates and cause of mortality for (a) adult and (b) juvenile whio in response to stoat . Survival rates were estimated using a Cormack-Jolly-Seber model in program MARK, while the cause of mortality was determined using visual assessment and necropsy of recovered remains. The number of individuals monitored under each treatment between 2000 and 2006 is given in parentheses.

particularly harsh 2004 winter. No remains of adult males were recovered, so it was not possible to assess the cause of adult male mortality.

Discussion

The results from the adaptive management programme confirm circumstantial evidence (i.e. Veltman et al. 1995, van Klink 2009) that stoats are responsible for the widespread decline of whio in beech forest systems. In the absence of stoat control, most pairs attempted to breed annually but none were able to successfully fledge young. Stoats were the primary cause of nest failure, with both eggs and young whio ducklings preyed upon. Stoat predation was also identified as the only cause of adult female mortality in the absence of stoat control. The use of large-scale, low-intensity stoat control greatly reduced the abundance index of stoats. This led to a significant increase in whio nesting success from 10 % in the absence of stoat control to 54 % in sites with stoat control, as well as an increase in the mean number of fledglings produced per pair.

The impact stoats have on nest survival is clear, but it is less apparent how other whio life history stages were affected. Because whio ducklings are nidifugous (Williams 1991), remains are rarely found and it was not possible to quantify the impacts of predation on this life history stage. However, stoat predation was found to be a contributing factor in duckling mortality, and no ducklings fledged when the mean annual stoat abundance index was greater than 5 %. Ducklings appeared to be particularly vulnerable during the 48 hour period after hatching when they remain in the nest and this is likely to be linked to increased olfactory cues due to broken eggshell in the nest (Prieto et al. 2003).

Whio survival varied significantly with age, with juveniles displaying lower survival. Juvenile whio, particularly males, were more likely to disperse outside the study area and were often found in high alpine tributaries where harsh winter conditions and a lack of predator control may have contributed to higher mortality rates. I was unable to assess the effectiveness of stoat control for juvenile whio as no ducklings fledged in

the absence of stoat control. However, juvenile whio were subject to low levels of stoat predation when stoat control was present.

Adult females had a slightly lower apparent survival rate than adult males and this was most likely caused by differences in vulnerability to stoats during the breeding season. Only adult females are involved with incubation (Williams and McKinney 1996) and they were found to be particularly vulnerable to stoat predation during this period. Female whio are slightly smaller than males (Williams 1991) and this may also lead to a greater predation risk. The cause of adult male mortality was difficult to quantify as no remains were located during the study period, although managers have subsequently found one adult male killed by a stoat (A. Smart, *pers. comm.*). The differences in apparent adult survival may also be due to differential dispersal, with several single adult males known to have emigrated from the study area. However, the initial sex ratio skew towards males noted in the study area suggests that the differences in survival are not simply an artefact of the sampling design.

The apparent survival rates for adult whio under the two management regimes differed in a counter-intuitive way, with higher apparent survival in the absence of stoat control. I suspect that this effect is primarily due to high emigration of adult males from the stoat control sites, coupled with the small sample size for the analysis. Eight of the 20 adult males initially banded in the trapped Clinton valley disappeared from the study site during the first winter, with many of them reappearing in neighbouring catchments in subsequent years. In comparison, almost all of the adult males present in the Arthur valley at the beginning of the study remained in this catchment during the period when stoat control was absent. These differences in emigration, combined with the small sample size, may have contributed to the calculated differences in the apparent survival rates between the two treatments. These results highlight the problems of working with threatened species where limited information is often available and population sizes are small. More research is required to determine if stoat control has a positive impact on the survival rates of juvenile and adult whio.

The impact of stoats on whio nesting success and survival is likely to have been inflated by the occurrence of two consecutive beech masts in 1999 and 2000. Stoat numbers vary significantly from year to year in New Zealand beech forests in response to the irregular production of high quantities of beech seed (King and McMillan 1982, Purdey et al. 2004). Beech mast events generally lead to elevated densities of rodents, causing a peak in stoat numbers the following summer (King 1983). This was noted in the Clinton valley, with high numbers of stoats trapped in the 2000/2001 and 2001/2002 summers. Whether a similar increase in stoat numbers occurred in the untrapped Arthur valley is unknown. There was no evidence, however, that the occurrence of mast events had a major impact on whio survival. Stoat control reduced stoat abundance indices to below 10 % in all years and preliminary results following a beech mast in 2006 suggest that whio were not negatively impacted when stoat control was in place (A. Smart, *pers. comm.*).

There has been an improvement in the productivity of whio in the presence of stoat control, but the number of pairs present within the study area has been slower to respond. Pair numbers decreased slightly in all three catchments in the year following the initiation of stoat control and this initial decline may be due to a lag associated with the one to two years that juveniles take to reach breeding age (Williams 1991) before they can replace adults that die. The Clinton valley experienced a greater initial decline than the other two catchments and this coincided with a period of high stoat capture associated with two beech mast events. How stoats responded to the beech masts in the Arthur valley is unknown, but I speculate that stoat numbers may be capable of reaching greater densities due to the lower rainfall (Department of Conservation, unpublished data) and more open topography in the Clinton valley (Christie et al. 2006). This effect may also explain the initial sex skew towards males in the Clinton Valley. When such a sex skew exists, the formation of whio pairs is limited by the number of females present in a catchment (Williams and McKinney 1996). However, if juvenile females continue to recruit into the study area, I expect the number of pairs in this population will increase with time.

Implications for conservation

A major new conclusion from my study is that the use of large-scale, low-intensity predator control arranged along rivers was sufficient to increase whio productivity in beech forest, even during periods of high stoat numbers. Predator control has been found to have positive impacts on the hatching success and adult survival rates of a number of bird species worldwide (Côté and Sutherland 1997, Dilks et al. 2003, Moorhouse et al. 2003, Bolton et al. 2007). However, many attempts at predator control have not been successful (Côté and Sutherland 1997) and these failures can generally be attributed to three main causes: 1) not targeting the primary agent of decline; 2) high rates of predator immigration during and after predator control; or 3) failing to adequately control all species within the predator assemblage. The large-scale, low-intensity stoat control used in the current study appears to be successful because it addresses all three areas of concern as identified below.

Identifying the primary agent(s) of decline is paramount to ensuring a successful predator control regime (Caughley 1994). Anecdotal evidence, including the known impacts of stoats on other New Zealand forest birds (Moors 1983) and the observed sex skew in many catchments, had suggested that stoats were a possible agent of decline for whio. Infra-red nest cameras and radio telemetry confirmed stoats to be the only mammalian predator of whio and whio nests at this study site, indicating that predator control should focus solely on this species. The large-scale, low-intensity predator control along a linear network used in the current study was capable of maintaining stoat densities at low levels throughout the study period, with whio pairs able to successfully produce fledglings when mean annual stoat abundance indices were less than 5 %.

The failure of many predator control regimes is often linked to high rates of predator immigration from surrounding unmanaged habitats (Kauhala et al. 1999). While stoats are capable of dispersing considerable distances at any time of year (King and McMillan 1982), there appears to be little movement of individuals between alpine environments and the forested valley floor (Smith and Jamieson 2005). Given the near-vertical topog-

raphy of the valley walls in this part of Fiordland National Park, the ability of neighbouring stoats to immigrate into the trapped area may be limited (Dilks et al. 2003), thereby increasing the effectiveness of the predator control regime in the study area. In areas of gentler terrain, a more intensive or widespread control effort may be required to maintain predator densities at the level observed in this study (Brown 2003).

Stoat predation on adult female whio may be a form of compensatory rather than additive mortality (Burnham and Anderson 1984), with stoats predating individuals that would have died from other, albeit more natural, causes (Banks 1999). In the presence of stoat control a number of adult females were killed by falcons, which may have increased in number in response to the reduced number of stoats. In addition to natural predators, other introduced mammalian predators may also contribute to whio mortality. Stoats were identified as the sole agent of decline for whio in Fiordland National Park, but ferrets (*M. furo*) and feral cats (*Felis catus*) may be important predators in some areas where whio are present (N. Riddler, unpublished data). It is likely that they have contributed to whio population declines to some degree, and alterations to the current predator control regime may be required to offer sufficient protection where these predators are present. Compensatory predation by predators not targeted through control measures has been found to be a problem in a number of systems (Banks 1999, Dion et al. 1999, Opermanis et al. 2005).

Unlike many other New Zealand species that can be protected on offshore islands (Towns and Ballantine 1993), whio conservation is reliant on the reduction of threats in mainland habitats due to a lack of suitable riverine habitat offshore (Chapter One). While mammalian predators will realistically never be eradicated from mainland sites without the use of predator-proof fences, the use of large-scale, low-intensity stoat control offers a long-term solution for declining whio populations. In addition, large-scale, low-intensity stoat control targeted at whio is likely to have wider community benefits, with a range of forest species known to respond positively to reduced stoat numbers (O'Donnell 1996, O'Donnell et al. 1996; Dilks et al. 2003, Kelly et al. 2005, Smith et al. 2005). However,

care needs to be taken that control measures do not result in a meso-predator release, whereby abundances of smaller predators such as rats increase, leading to a negative impact on other threatened species (Tompkins and Veltman 2006).

I found that large-scale, low-intensity predator control can reduce the density of predators to a level where the increased productivity and survivorship of threatened species is detected (Dilks et al. 2003, Pryde et al. 2005). Providing that predator densities can be maintained below the threshold required for the persistence of threatened species (Basse et al. 1997, Sinclair et al. 1998), large-scale, low-intensity control of some predator species can lead to increased productivity for threatened species, making it a valuable tool for conservation managers.

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Chapter Three

Large-scale predator control increases population viability of a rare New Zealand riverine duck

Abstract

The introduction of mammalian predators to oceanic islands has led to dramatic declines in the abundance of many native species. Conservation management of these species often relies on low cost predator control techniques that can be implemented over large scales. Assessing the effectiveness of such management techniques is difficult, but using population viability analyses (PVA), which identify the population growth rate (λ) and extinction risk of threatened species, may offer a solution. PVA provide the opportunity to compare the relative effectiveness of different management options and can identify knowledge gaps to prioritise research efforts. I used PVA to assess the population viability of whio (*Hymenolaimus malacorhynchos*), a rare riverine duck endemic to New Zealand. Current populations are threatened by introduced mammalian predators and are rapidly declining in both distribution and abundance. Whio conservation management is dominated by large-scale, low-intensity predator control, targeting introduced stoats (*Mustela erminea*). There is evidence that such control increases whio productivity but it is unknown if this increase is sufficient for long-term population persistence. I undertook a stochastic PVA to assess the viability of whio populations under different management scenarios using data obtained from a six-year study of whio demographic responses to predator control. My models showed that populations with no predator control and low productivity will rapidly decline to extinction. Increasing productivity through predator control increased population viability but populations still showed a declining trajectory. A perturbation analysis showed the growth rate of whio populations was largely driven by

adult survival. Therefore, future research should target obtaining more robust estimates of adult survival, particularly how it is affected by predator control. Overall, my analysis indicates that large-scale, low-intensity predator control increases the short-term viability of whio populations but is insufficient for long-term population persistence.

Introduction

The introduction of mammalian predators to oceanic islands has led to dramatic declines in the abundance of native species that have often evolved in the absence of such predators (Courchamp et al. 2003, Blackburn et al. 2004). As a result, active conservation management is required to preserve or restore populations of threatened species (Clout 2001). Such management typically focuses on predator control, which ranges in intensity from seasonally-targeted control during periods of high prey vulnerability, to complete eradication (Côté and Sutherland 1997, Courchamp et al. 2003). Eradication is frequently impossible over large areas and with some suites of predators (Courchamp et al. 2003), so development of reliable, low-cost techniques to reduce predator abundance over large areas is paramount for many conservation programmes. Assessing the effectiveness of such management techniques is frequently hampered by limited information about the threatened species and their long-term prospects. Population modelling is useful in such situations and here I assess the effectiveness of large-scale, low-intensity predator control with population viability analysis (PVA).

PVA estimates the population growth rate (λ) and risk of population extinction, and has been used to guide conservation management for over 25 years (Shaffer 1981). PVA models are capable of modelling relatively complex systems (Heppell et al. 1994) but can also cope with sparse datasets (Heppell et al. 2000), making them ideal for conservation management problems. There is often doubt associated with the absolute results of PVA models due to parameter uncertainty or model realism (McCarthy et al. 2001, McCarthy et al. 2003), but relative comparisons of potential management options offer a platform

for managers to make more informed decisions (Coulson et al. 2001). In particular, PVA can be used to assess the sensitivity of the population growth rate or risk of extinction to changes in demographic rates. Such information can be valuable for directing conservation effort to the most influential life history stages or to highlight knowledge gaps that can help to focus future research efforts (Crouse et al. 1987). This is particularly useful when management is conducted over large scales and its long-term effectiveness is not immediately apparent. PVA can also be used to assess the relative impacts of different management scenarios, providing guidance to rationalise management. Even in the presence of high uncertainty around parameter estimates, the predictions generated are useful for threatened species management where immediate action may be required to prevent further declines in already reduced populations.

Terrestrial conservation efforts in New Zealand are dominated by lethal predator control aimed at reducing predator densities over large areas of habitat (Clout 2001). The endemic riverine whio, or blue duck (*Hymenolaimus malacorhynchos*), is the focus of intensive conservation management through large-scale, low-intensity predator control along rivers. Whio currently occupy only a small portion of their historical range, due to predation by introduced mammalian predators and habitat modification (Chapter One), and the total population is likely less than 2,500 individuals (van Klink 2009). Many whio populations are rapidly declining and introduced stoats (*Mustela erminea*) have been identified as the main agent of decline (Whitehead et al. 2008). Current predator control measures dramatically improve whio nesting success and duckling survival, but their effect on other life history stages is less well known (Whitehead et al. 2008). Uncertainty in estimates of demographic rates is partially due to the small size of the monitored populations. Further monitoring would improve estimates of demographic rates but is costly and populations may continue to decline while further data are being collected, if current management is inadequate. Thus, it is important to determine whether the observed increases in whio productivity associated with predator control are enough to lead to viable whio populations.

I developed a model to assess long-term whio population viability under two management scenarios: with and without large-scale, low-intensity predator control. In addition, I assessed the relative influence of individual demographic rates and initial population size on population viability, and the sensitivity of the model to changes in mean parameter values. Since little is known about the impacts of predator control on most whio life-history stages, I did not attempt to make specific predictions about the absolute risk of extinction but have instead assessed changes in the relative risk of extinction. This approach is particularly useful when there is high uncertainty regarding the demographic data used (Beissinger and Westphal 1998, Ralls et al. 2002, McCarthy et al. 2003).

Methods

Study area

Whio were monitored in three river valleys in Fiordland National Park, New Zealand (midpoint 44°S, 167°E) over a six-year period (2000-2006). These valleys were subject to experimental stoat control: stoat control was present in the Clinton valley for the first three years of the study, while there was no stoat control in the neighbouring Arthur valley. Stoat control was established in the Arthur valley in April 2003 and monitoring continued in both valleys for an additional three years. The Cleddau valley was also included in the study in October 2003 after stoat control was established through a community-driven initiative. Details of whio monitoring and stoat control are described by Whitehead et al. (2008).

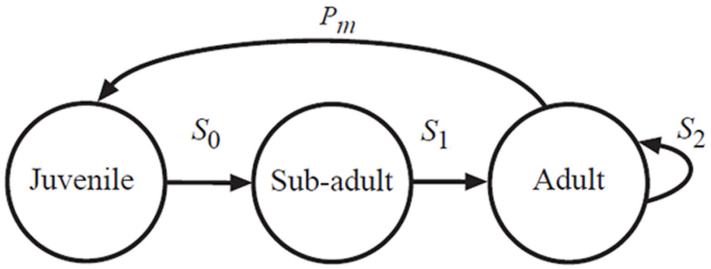
Stochastic Leslie matrix model

I used a three stage Leslie matrix, which operated on an annual time step to model whio populations (Leslie 1945). The model was constructed in R (Version 2.1.1, R Development Core Team 2005) and consisted of three life history stages: juveniles, sub-adults and adults (Figure 1). I define juveniles as whio in their first nine months after fledging, and

sub-adults as non-breeding whio in their second year. Demographic rates were estimated using data from the six-year paired catchment study described above (Table 1; Whitehead et al. 2008). Whio form long-term monogamous pair bonds, with excess males holding territories but not contributing to population growth (Eldridge 1986, Williams and McKinney 1996). Consequently, only female population dynamics were modelled. Virtually all adult females form pairs when mates are available (Williams and McKinney 1996, Whitehead et al. 2008), so the number of adult females present in the population is approximately equivalent to the number of adult pairs.

The model counted the number of adult females alive at the beginning of the breeding season using parameters from the previous year including adult abundance, adult survival and sub-adult recruitment. The initial age distribution of birds for each model run was set to a stable age distribution derived from the right eigenvector (w) of a deterministic version of the population model constructed with the mean input parameters (Table 2; Caswell 2001). Female sub-adult whio were assumed to recruit to the breeding

a)



b)

$$A_m = \begin{pmatrix} 0 & 0 & P_m \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2 \end{pmatrix}$$

Figure 1. Population model structure (a) and transition matrix (b) used to model two management scenarios (m) for whio in Fiordland National Park. The pre-breeding Leslie matrix model operates on an annual time step and consists of three female life stages: juveniles (S_0), sub-adults (S_1) and adults (S_2). Annual productivity (P_m) is a function of the number of breeding females, egg production, and nest and duckling survival (see Equation 1 in text). Values for model parameters are shown in Table 1 and were derived from a six-year field study (Whitehead et al. 2008).

population when two years old (Whitehead et al. 2008). I assumed density-independent growth and a closed population as little is known about patterns of immigration, emigration and density-dependence in whio (Whitehead et al. 2008). Given the low density of current whio populations in these valleys (0.18 - 0.27 pairs per linear km of river), it is also unlikely that any density-dependent effects would be expressed in the range of population sizes considered in my model.

In the model, annual productivity (P_{mt}), or the number of female juveniles produced per female per year, at time t under a given management regime (m) was the product of the proportion of breeding females in the population (b_t), egg production (e_t), and nest (n_{mt}) and duckling survival (S_{dmt}). I assumed an equal sex ratio (d_f) at hatching. Thus, the equation representing productivity was:

$$P_{mt}=b_t n_{mt} \frac{e_t}{d_f} S_{dmt} \quad (1)$$

In the study area, 65 ± 9 % (mean ± se) of adult females bred annually, producing 4.3 ± 0.2 eggs per nest. Nest survival for whio was significantly lower in the ab-

Table 1. Mean (± se) annual per capita demographic parameters incorporated into stochastic female population models of whio under two management scenarios. The no stoat control and stoat control scenarios are based on data collected from a six-year study of whio demographics in response to large-scale, low-intensity predator control (Whitehead et al. 2008). See Methods for further details.

Model Parameters	No stoat control	Stoat control
Eggs per nest	4.3 ± 0.2	4.3 ± 0.2
Breeding females (%)	65 ± 10	65 ± 10
Nest survival	0.10 ± 0.02	0.54 ± 0.01
Duckling survival	0.13 ± 0.05	0.65 ± 0.05
Juvenile survival	0.51 ± 0.14	0.51 ± 0.14
Sub-adult & adult survival	0.74 ± 0.09	0.74 ± 0.09

sence of stoat control, with 10 ± 1.9 % nests hatching at least one duckling compared to 54 ± 0.5 % when stoat control was present (Whitehead et al. 2008). No ducklings survived to fledge in the absence of stoat control. However, this result was based on a small sample size (N = 4 hatchlings) and ducklings are known to fledge in other untrapped catchments (A. Whitehead, unpublished data). Therefore, I used an estimated duckling survival rate of 0.13 ± 0.05 in the absence of stoat control. Duckling survival in the presence of stoat control was 0.65 ± 0.05.

No juveniles were present in the population in the absence of stoat control, so I was unable to determine juvenile survival under those conditions. Therefore, the juvenile survival rate (S_0) of 0.51 ± 0.14 estimated under stoat control was used in both model scenarios. Annual survival rates for adult female whio were 0.80 ± 0.10 and 0.67 ± 0.07 in the absence and presence of stoat control, respectively (Whitehead et al. 2008). However, these estimates were likely biased by small sample sizes and were not significantly different (Whitehead et al. 2008). Therefore, I used the pooled value of 0.74 ± 0.09 (S_2) for adult survival as this provides a conservative, yet likely realistic estimate of adult survival. Sub-adult survival (S_1) was not calculated in the Fiordland study. However, observations of whio on the Manganui-a-te-ao River suggest that sub-adult and adult survival are similar (Williams 1991), so I used the pooled adult survival rate for both adults and sub-adults.

Table 2. Stable age distribution for whio populations under two management scenarios. Values were calculated from the right eigenvector (*w*) of deterministic matrices for each scenario and are expressed as percentages of the total population.

Life history stage	**No stoat control**	**Stoat control**
Juvenile	2.42	29.42
Sub-adult	1.64	15.75
Adult	95.94	54.83

The average number of eggs per nest was calculated by drawing a random sample from the known distribution of eggs per nest within the population. Inter-annual variation was incorporated into all demographic rates by randomly selecting from beta distributions defined by the mean and variance of each parameter. I also included demographic stochasticity using binomial probability distributions at each time step (White 2000).

I created two model scenarios based on the demographic data from the Fiordland population (Table 1); a scenario without stoat control that had low productivity, and a stoat control scenario with high productivity. All other mean demographic rates were held constant across the two matrices.

Population Growth Rate (λ)

I estimated mean population growth rate (λ) under the two management scenarios by running each scenario model for 10,000 iterations. To assess the influence of demographic rates on population growth rate and develop a tool to help managers assess the requirements of management, I also compared models comprising all possible combinations of productivity, juvenile, and sub-adult/adult survival

Time to extinction

I assessed the risk of extinction for populations under the two management scenarios by calculating the median time to extinction (i.e. the timeframe in which 50 % of modelled populations became functionally extinct). I used a quasi-extinction threshold based on the minimum effective population size (Ne = 50), whereby a population was considered extinct if the number of females dropped below 25. Each simulation was run for 10,000 iterations to estimate the median time to extinction under each scenario, with individual iterations run for 100 years or until the population became quasi-extinct. Initial population sizes ranged from 5 – 50 adult females, with the initial stable age distribution calculated from the appropriate deterministic matrix.

Perturbation Analysis

A perturbation analysis was conducted to assess how small changes in the input parameters of the projection matrices altered the resulting population growth rate and time to extinction (Caswell 1978). The analysis was performed by multiplying the mean value of individual model parameters by ± 10 % while holding the remaining parameters in the model constant. This has the effect of shifting the distribution of the parameter by 10 % while still incorporating the measure of variation around the mean. The models were run 10,000 times to estimate the effect of the 10 % parameter change on the population growth rate and time to extinction. Parameters assessed included nest, duckling, juvenile, sub-adult and adult survival rates, as well as the proportion of adult females breeding annually.

Results

The scenarios in the absence and presence of stoat control both resulted in declining mean population growth rates for whio, with mean (± se) λ values of 0.74 ± 0.0002 and 0.95 ± 0.0002, respectively (Figure 2). Figure 3 shows, in contour plots, those combinations of whio demographic rates required to achieve a stable population (λ = 1.00). As expected, decreasing the value of one demographic rate required higher rates for remaining parameters to maintain a stable population growth rate. The graphs enable managers to assess the improvements needed in demographic rates to reach a stable population. For example, the scenario without stoat control (Figure 3a) used low estimates of productivity (0.02 fledglings per pair), resulting in a negative growth rate (λ = 0.74). A stable population could be achieved by a large increase in productivity from 0.02 to 0.70 fledglings per pair. However, it would not be possible to achieve population persistence by increasing juvenile, sub-adult and adult survival rates without an associated increase in productivity. The stoat control scenario (high productivity: 0.51 fledglings per pair) also had a negative growth rate (λ = 0.95; Figure 3b) but a stable population could be achieved by increas-

ing productivity (0.51 to 0.70 fledglings per pair) or sub-adult and adult survival (0.74 to 0.80). It is important to note that the slopes of the isolines in Figure 3 are not linear, indicating that the effect of individual demographic rates on λ depends on the value of the rates themselves.

Growth rates were most sensitive to changes in mean adult survival in both scenarios (Figure 4). Thus, a 10 % decrease in mean parameter values resulted in declining populations (λ < 1) for all perturbed parameters. In the stoat control scenario, a 10 % increase in mean parameter value of adult survival resulted in increasing populations (λ = 1) but this effect was not seen with the other parameters. No increase in a perturbed parameter led to a stable or increasing population (λ ≥ 1) in the scenario without stoat control.

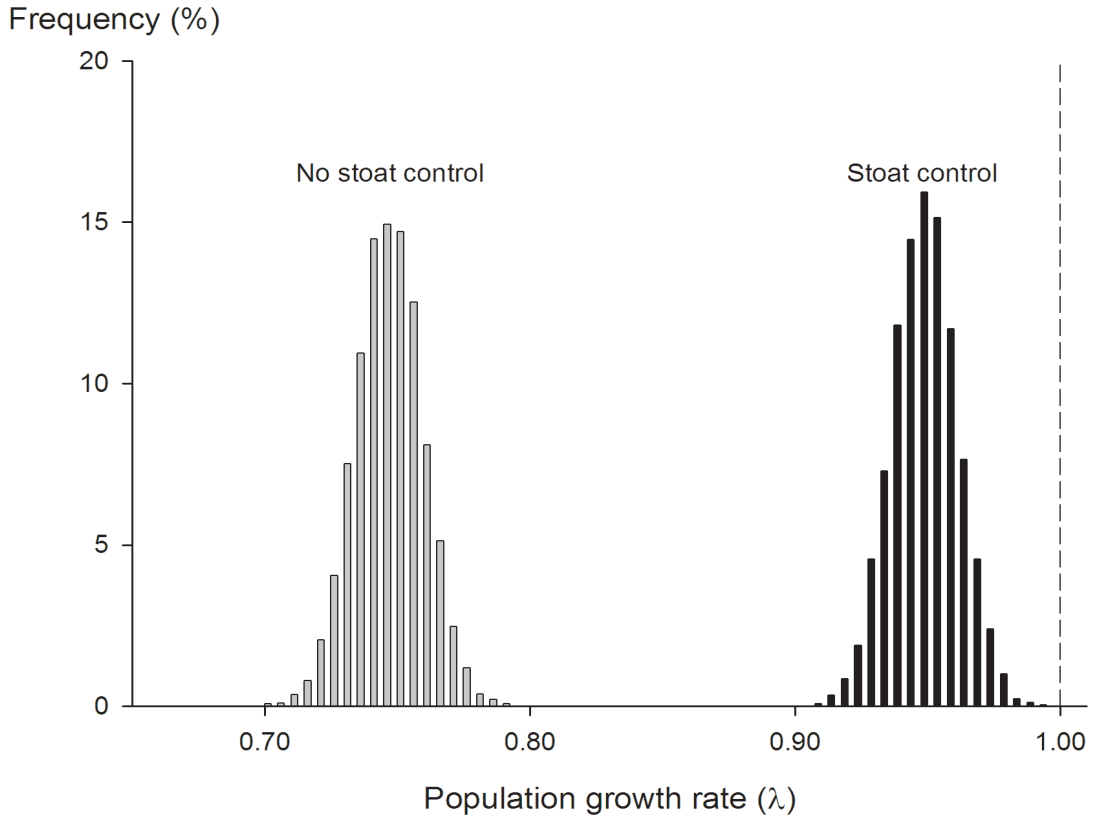


Figure 2. Distribution of population growth rates (λ) from a stochastic population model of whio populations under two different management scenarios: no stoat control and stoat control. Distributions are based on 10,000 simulations. The dashed line represents a stable population (λ =1).

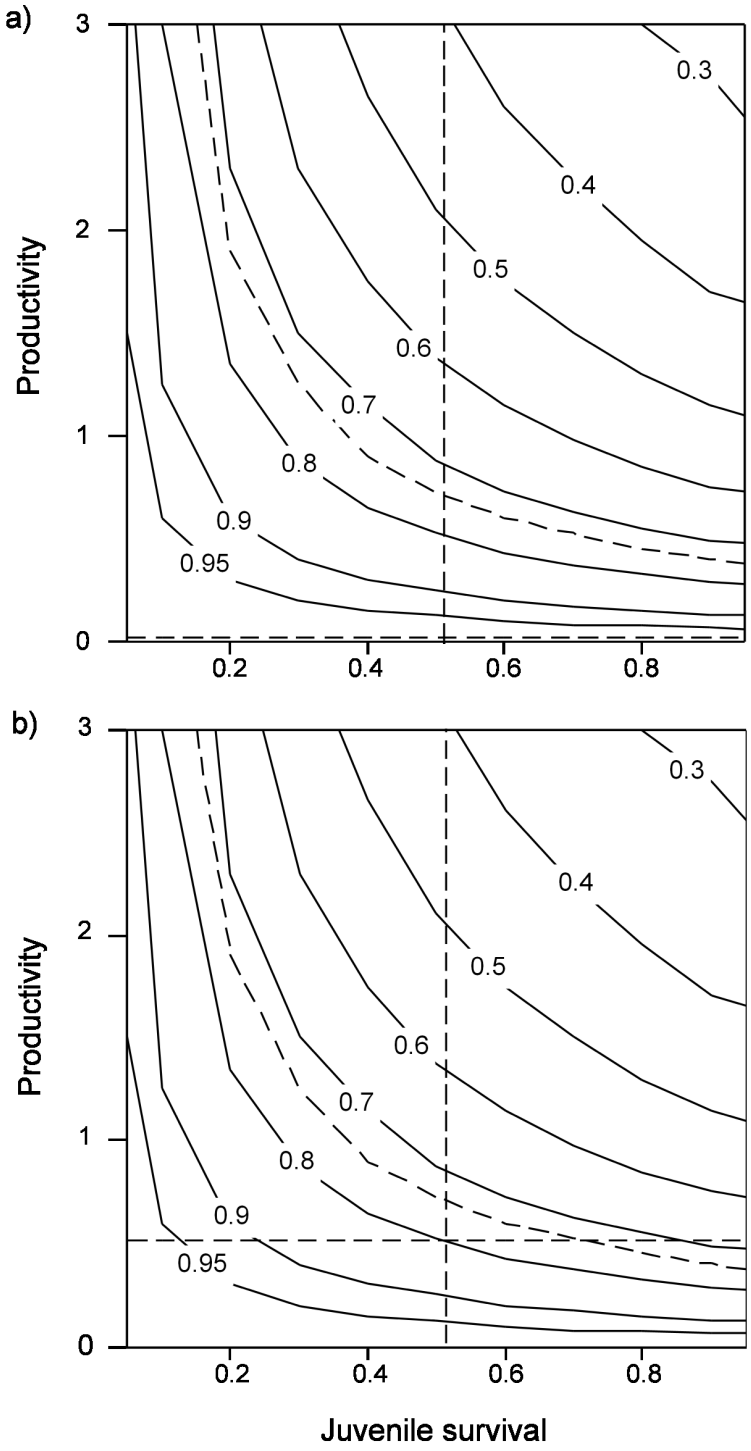


Figure 3. Contour plots of the mean whio population growth rate (λ) under different combinations of mean productivity, juvenile, sub-adult and adult survival. The contours are labelled by the mean sub-adult/adult survival rate and describe the mean productivity and juvenile survival rates necessary to achieve a stable population (λ = 1). In each of the three plots the dashed lines represent the demographic parameters used in the model for the two management scenarios: (a) no stoat control and (b) stoat control. For the two scenarios depicted, a stable population is only achieved when productivity and juvenile survival both intersect on a sub-adult/adult contour.

Considerable variation in the median time to extinction was found between the two scenarios (Figure 5). In the scenario without stoat control, whio had a high risk of extinction with 50 % of populations predicted to be extinct within three years, irrespective of initial population size (Figure 5a). Perturbations of adult survival led to relative changes in time to extinction of up to 50 %, while independent 10 % perturbations of the other demographic parameters had no effect on time to extinction. There was a lower risk of extinction under the stoat control scenario, with a median time to extinction of 12 years for a population of 50 pairs (Figure 5b). Increasing adult survival by 10 % increased the time to extinction considerably (up to 633 %), particularly as the initial population size increased. In comparison, a 10 % decrease in adult survival resulted in a 50 % decrease in time to extinction. The median time to extinction ranged approximately 33 % above and 20 % below that predicted for the stoat control scenario due to independent 10 % perturbations of nest, duckling, juvenile and sub-adult survival rates.

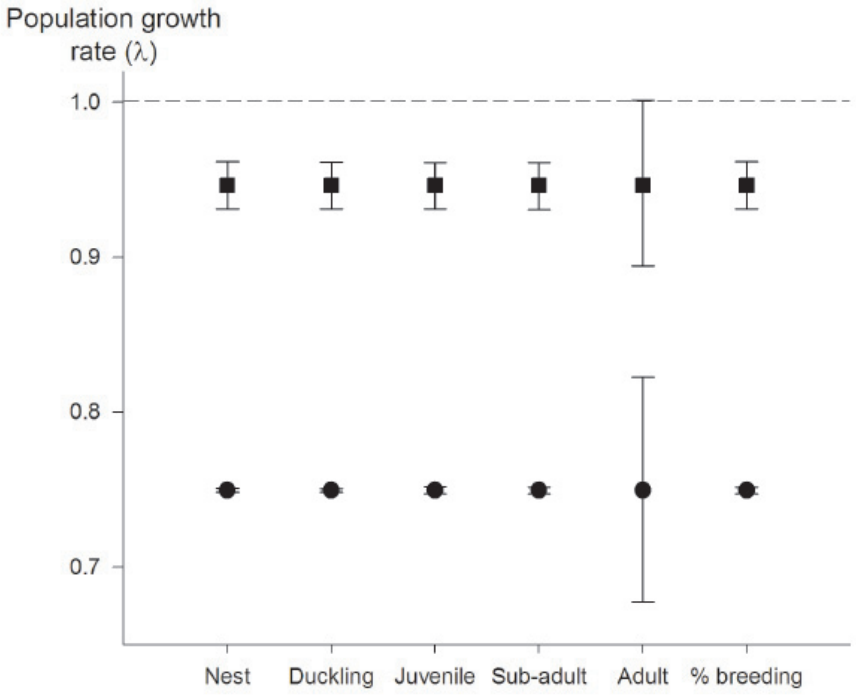


Figure 4. Sensitivity of the mean population growth rate (λ) to 10 % perturbations of the mean parameters in the population model under two management scenarios for whio conservation: no stoat control (●) and stoat control (■). The symbols represent the mean population growth rate of the baseline matrix for each scenario, while error bars show the mean change due to the perturbations. The dashed line represents the population growth rate of a stable population (λ = 1).

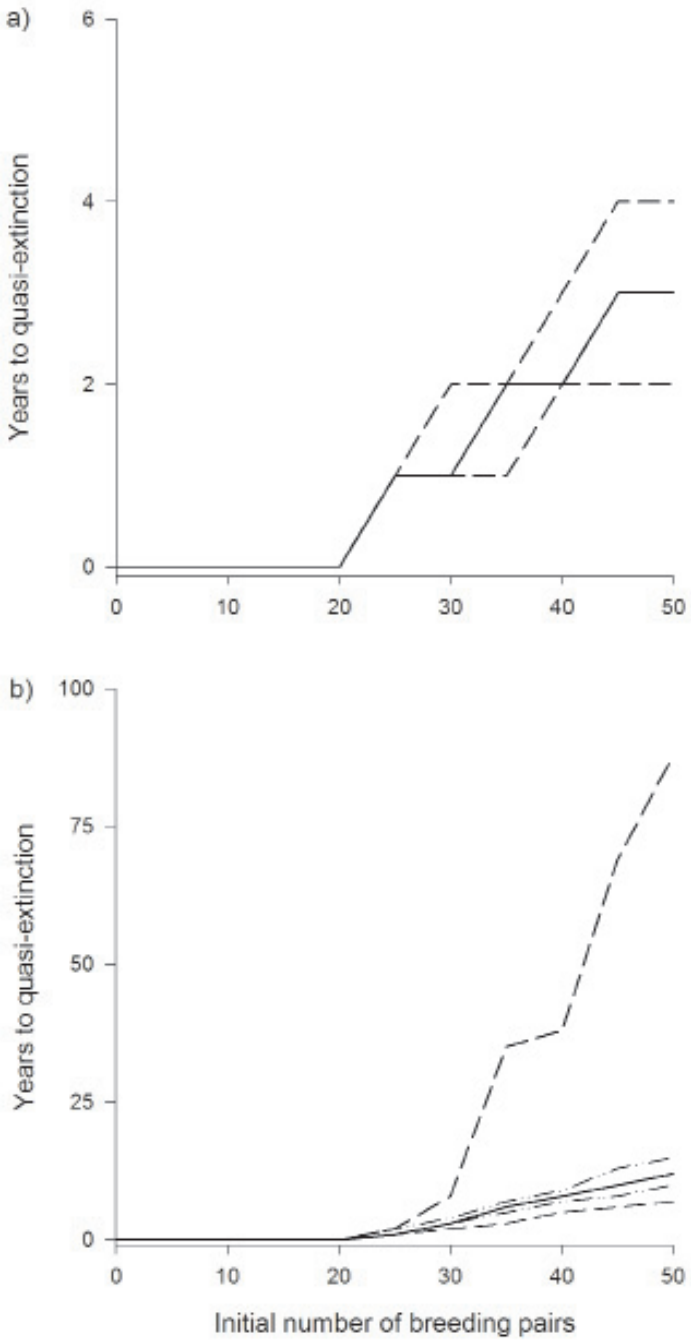


Figure 5. The predicted median time to quasi-extinction of whio populations in relation to the initial number of breeding pairs under two management scenarios: (a) no stoat control and (b) stoat control. Sensitivity of the time to extinction (dashed lines) was assessed using 10 % perturbations of entries in the population projection matrix. In the stoat control scenario, time to extinction showed similar responses to independent perturbations of nest, duckling, juvenile and sub-adult survival, as well as the proportion of adult females breeding. In the scenario without stoat control, only 10 % perturbations of adult survival altered the time to extinction. Therefore, the response of time to extinction is only shown for independent perturbations to adult (— —) and nest survival (stoat control scenario only; — · · —) for ease of interpretation.

Discussion

This PVA has provided important insights into the performance of managed whio populations that were not obvious from short-term monitoring. Although PVAs are more reliable when used to compare the relative extinction risk of different scenarios than when used to estimate absolute extinction risk, it is nonetheless worthy of note that even the stoat control scenario has a predicted population growth rate of less than one. This indicates that although predator control has reduced whio extinction risk, my best estimate of the population growth rate suggests that the position of whio is still precarious even when whio predators are controlled.

My model has shown that whio populations in the absence of stoat control with low productivity have low growth rates and a high risk of extinction. Low whio productivity is typically caused by stoat predation of nests, resulting in the loss of eggs or young ducklings (Whitehead et al. 2008). Whio populations exposed to high levels of stoat predation in the absence of stoat control are likely to experience rapid localised extinctions. Large-scale, low-intensity predator control has been shown to improve whio productivity (Whitehead et al. 2008) and my models show that this leads to higher population growth rates. However, the major finding of my assessment is that populations are only viable when adult female survival rates are higher than currently predicted. Estimates of adult whio survival in Fiordland are based on small sample sizes and while predator control is known to reduce the rate of stoat predation on adult females, I did not measure a decrease in overall mortality (Whitehead et al. 2008). Compensatory mortality by increased native falcon (*Falco novaeseelandiae*) populations in the presence of stoat control may explain part of this counter-intuitive result (Whitehead et al. 2008) but further monitoring is required to develop better mortality estimates and better understanding of the relationships between predator control and adult whio survival. This is particularly important given the high sensitivity of the population growth rate to adult survival, a phenomenon common to many long-lived species (Boyce 1992, Sæther and Bakke 2000, Sæther et al. 2005). By

finding that current predator control may not be sufficient to ensure whio persistence, my model indicates the value of evaluating the long-term usefulness of large-scale predator control.

My models were relatively insensitive to components of whio productivity (% of breeding adults, nest survival and duckling survival), but the importance of management efforts directed at these life history stages should not be underestimated. Productivity of whio populations in the absence of stoat control is extremely low (Whitehead et al. 2008) and the juvenile, sub-adult and adult survival rates required to reach a stable population under such conditions are likely to be close to or above the biological limits for whio survival. Therefore, it is unlikely that effective conservation management for whio can be undertaken without improving productivity in conjunction with other demographic rates. My models highlight the importance of understanding the cause of decline and the response of threatened populations to management of the causal factor. Without such knowledge, managers run the risk of developing ineffective management regimes that may lead to further declines and waste limited resources (Crouse et al. 1987, Doak et al. 1994, Keedwell et al. 2002).

Estimates of the relative time to extinction allow managers to assess the relative effectiveness of different management scenarios and inform decision-making. The New Zealand Department of Conservation's Whio Recovery Group has set 50 pairs as the minimum target for a secure whio population within a management area (van Klink 2009), equating to approximately 182 individuals under management. My analysis suggests that a population of this size has a high long-term risk of extinction under current management conditions, but is relatively more secure than an unmanaged population. This provides managers with confidence that current management is improving population viability but highlights the need for further development of management methods.

PVA models provide a useful guide to managers but they should be used cautiously in conservation planning. Extinction analyses based on short-term studies can underestimate the risk of extinction, particularly for small populations (Caughley 1994). The

occurrence of occasional catastrophic events may increase significantly increase this risk (Shaffer 1981, Thomas 1990, Reed et al. 2003). Such factors could be of particular concern for whio populations found in New Zealand beech (*Nothofagus*) forest. These forests are characterised by periodic autumn mast events where large quantities of seed are produced every three to five years (Wardle 1984), stimulating a dramatic increase in introduced rodents numbers (*Mus musculus, Rattus exulans, R. norvegicus* and *R. rattus*), and then stoat numbers the following summer (King 1983). Beech masting events have led to increased rates of mammalian predation on a wide range of New Zealand bird species (Murphy and Dowding 1995, White and King 2006). Whitehead et al. (2008) found no evidence of increased whio mortality during such irruption events in the presence of predator control. Nevertheless, high stoat numbers likely have an impact on all whio life-history stages, particularly when beech masting events occur in consecutive years, leading to high stoat numbers over an extended period. An improved understanding of the response of whio populations to stoat irruptions is required to accurately assess the effectiveness of large-scale, low-intensity stoat control for whio management.

Model limitations

Population models are necessarily a distilled reflection of reality and, therefore, the results may be distorted by factors that have been inadequately modelled or not included (McCarthy et al. 2001). My simple model utilised known demographic rates and did not include density-dependence or dispersal, both of which are likely to operate in real whio populations. This may have reduced the ability of the model to capture population dynamics in their entirety, but current understanding of how these factors operate in small whio populations is poor. Rates of inter-catchment dispersal by whio are unknown but dispersal is more frequently observed in juveniles and adult males than adult females (Whitehead et al. 2008). Because my models only considered the female population dynamics, it is unlikely that the absence of dispersal in the model had a significant impact on the predicted population dynamics at low whio densities. However, dispersal patterns

are likely to change with population density (Matthysen 2005, Carr et al. 2007). Henderson (1994) noted a decline in whio adult survival with increasing density in the densely populated Manganui-a-te-ao River, but no evidence of density-dependent regulation was observed in Fiordland, where the density of birds was much lower (Whitehead et al. 2008). Small recovering populations of threatened species are unlikely to be strongly regulated by density dependence in the short-term (Taylor et al. 2005). Ignoring density dependence is probably appropriate when the aim is to assess the relative viability of a recovering population with a low initial density, rather than the size the population might attain in the longer term.

General implications for conservation managers

Short-term monitoring to assess the effectiveness of management can be misleading if observed increases in demographic parameters do not lead to populations that are viable long-term. PVA offers a solution to this problem by utilising available demographic data to make predictions of long-term population viability, providing valuable information that may not be apparent from short-term monitoring. My analyses for whio indicate that increased productivity due to large-scale, low-intensity predator control results in improved population viability but the long-term risk of extinction remains high.

Increasing the accuracy of population viability estimates often requires access to long-term datasets or more accurate demographic information. However, such information typically is not available for threatened species and populations may continue to decline while further data is collected if management is ineffective. To reduce the potential impacts of inaccuracies due to a short-term dataset, I refrained from predicting absolute time to extinction due to high uncertainty around the value of these outputs (McCarthy et al. 2003). Instead, I assessed the relative effectiveness of different management options. PVA has an important role in identifying knowledge gaps in the demography of threatened species, helping to prioritise areas for future research. I identified areas where future research should be targeted to better our understanding of whio population dynam-

ics, particularly with regard to adult survival. My analysis has highlighted the importance of coupling this information with knowledge of the major causes of decline to ensure that management is targeted at the appropriate life history stages (Crouse et al. 1987, Doak et al. 1994, Beissinger and Westphal 1998), thereby maximising conservation benefits.

In this study, low-intensity predator control over a large scale has led to significantly increased whio population growth but there is still uncertainty about whether the increase is sufficient to ensure the species' long-term survival.

Acknowledgements

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Chapter Four

More ducks for your bucks: a multi-scale assessment of habitat quality-fitness relationships to enhance management of a threatened riverine duck

Abstract

With strong competition for limited funding, species conservation should be concentrated in areas of high quality habitat where individuals make the greatest contribution to population growth. Populations in high quality habitat are more likely to persist long-term due to increased survival and/or reproductive rates, and should respond to conservation management more quickly than populations in poor habitat. I assessed the relationships between habitat characteristics, occupancy and fitness for a threatened New Zealand riverine duck, the whio (*Hymenolaimus malacorhynchos*), at two spatial scales to identify areas of high quality habitat. At the broadest geographic scale, the occupancy of whio territories was positively correlated with reproductive output, and population density was a useful indicator of habitat quality. Smaller scale analysis revealed spatial differences in the relationships between fitness measures, indicating there were inherent differences between populations in the North and South Islands of New Zealand that may not be directly linked to habitat quality. I recommend that management plans for whio conservation be island-specific, with priority sites concentrated in warm, stable rivers to maximise conservation gains. My research highlights the importance of considering multiple measures of fitness at multiple spatial scales when assessing habitat quality for threatened species management.

Introduction

Conservation is resource-limited, with many species and habitats competing for limited funding (Balmford et al. 2003). This reality has led to the development of methods to prioritise species and ecosystem conservation to increase the effectiveness of conservation efforts (Early and Thomas 2007, Bottrill et al. 2008, De Wan et al. 2009). Such research has included identifying biodiversity hotspots and areas of intact wilderness (Klein et al. 2009), prioritising sites based on the predicted cost of management (Brooke et al. 2007), and assessing the effectiveness of monitoring and management options for single species (Bakker and Doak 2009). One issue that is common to all of these approaches is evaluating the quality of habitat to be managed. Ideally, management efforts should be concentrated in areas of high quality habitat where individuals will make the greatest contribution to population growth (Sergio and Newton 2003). Populations in high quality habitat are more likely to be persistent due to increased survival and/or reproductive rates (Johnson 2007), and should respond to conservation management more quickly than populations in poor habitat. This means that fewer resources should be required to reach the desired outcome, providing opportunities to reallocate resources elsewhere (Fairburn et al. 2004).

The quality of habitat for a given species is determined by the ability of the environment to provide the resources and conditions necessary for individual and population persistence (Hall et al. 1997). Based on ecological theory, individuals should select habitats that confer the greatest fitness (Fretwell and Lucas 1970), although there are circumstances when habitat selection may be non-ideal or maladaptive (Battin 2004, Arlt and Pärt 2007). This can occur when the cues used by individuals to select habitat are not correlated with habitat quality (i.e. ecological traps; Battin 2004), or when measures of fitness, such as reproduction and survival, respond differently to habitat gradients (Kristan 2007). In such cases, the density of individuals may not be representative of habitat quality (van Horne 1983), meaning traditional methods of selecting management

sites based on population density alone may be inappropriate. Therefore, understanding the relationships between habitat quality, variation in fitness, and population density for threatened species should be a research priority.

Habitat quality can vary both spatially and temporally, and both factors can influence an individual's ability to select high quality habitat (Johnson 2007). Organisms may use cues at a variety of spatial scales to select habitat, ranging from broad-scale patterns in landuse to fine-scale changes in local conditions. These fine-scale habitat choices are important but it is usually not possible to conserve populations at the scale of individual territories (Kristan 2003). Therefore, assessments of habitat quality for conservation purposes need to be at scales that are appropriate for making management decisions. I investigated the relationships between habitat quality, habitat use and fitness in a threatened riverine duck at two spatial scales relevant to populations by identifying areas of high quality habitat that could be targeted for conservation management.

Whio (blue duck, *Hymenolaimus malacorhynchos*) are a riverine duck, endemic to New Zealand. They were historically widespread but are now restricted to small, fragmented populations due to habitat modification and predation by introduced mammals, particularly stoats (*Mustela erminea*; Chapter One, Whitehead et al. 2008, Whitehead et al. in press). Conservation management for whio is dominated by lethal predator control, which significantly increases whio productivity (Whitehead et al. 2008). This means there is considerable potential to expand the current range of whio using predator control. However, large-scale predator control is expensive (Choquenot 2006) and limited resources for conservation mean that managers must prioritise efforts to sites that provide the best value for money.

Whio pairs are monogamous and highly territorial, defending a stretch of river year-round (Williams and McKinney 1996). Therefore, the habitat resources within the territory are likely to influence whio fitness directly. Elevation, channel width, stream stability, substrate composition and riparian vegetation are known to influence whio presence on a river (Chapter One, Fordyce 1976, Collier et al. 1993, Collier and Wakelin 1996,

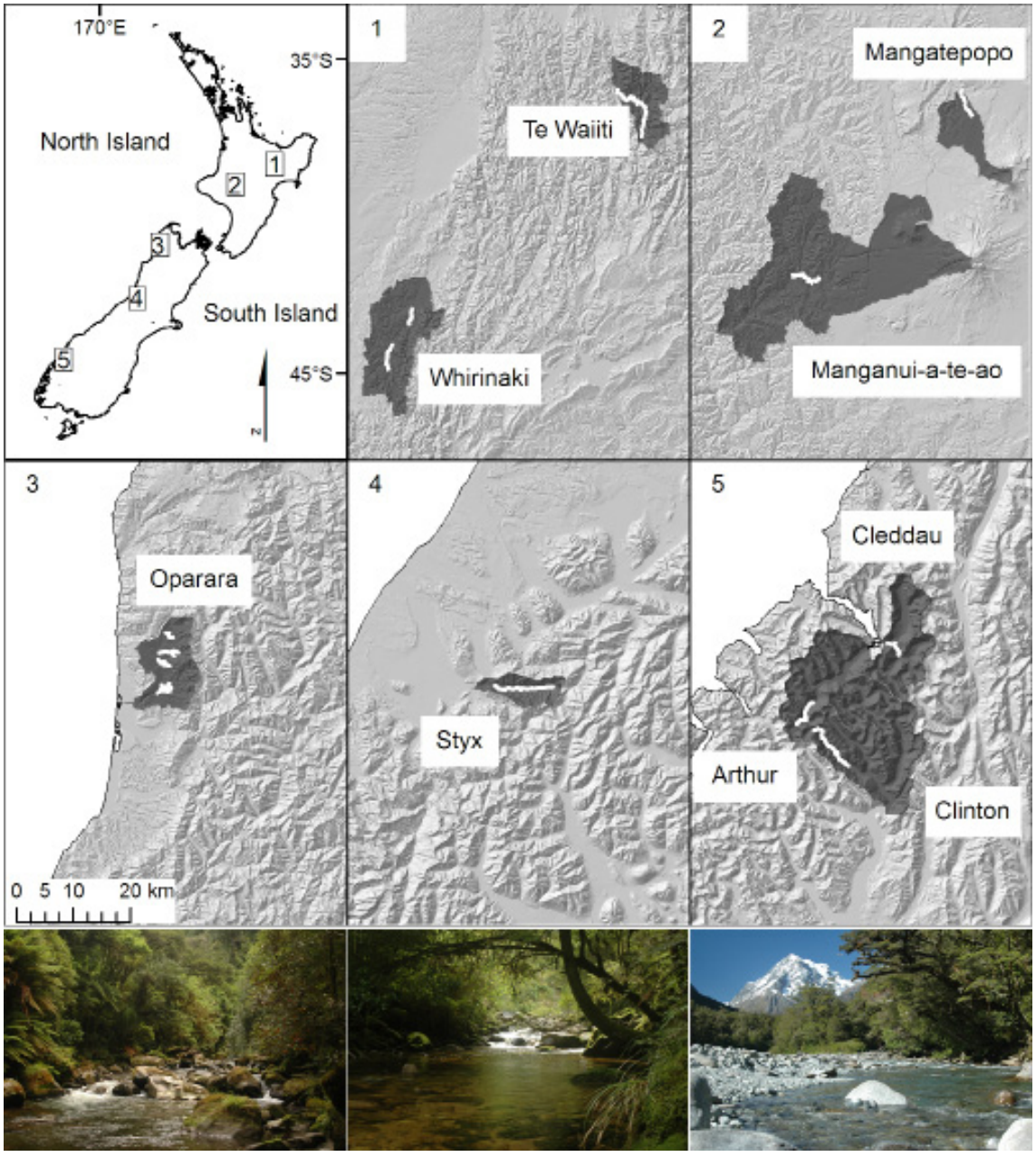

Figure 1. Nine New Zealand river catchments where whio habitat was surveyed during the 2007/2008 austral summer. All catchments have large-scale mammalian predator control for whio conservation run by the New Zealand Department of Conservation. Catchments are shown by dark shading and sampled reaches are shown in white. Panels one to five are drawn to the same scale. Photos show representative whio habitat on the Whirinaki, Oparara and Cleddau Rivers (left to right; Photos. A. Whitehead).

Baillie and Glaser 2005), but the relationships between whio habitat, fitness and population density have not been assessed (but see Godfrey et al. 2003). Thus, to ensure cost-effective management, predator control should be directed at habitats that maximise whio fitness, and it needs to be determined how fitness is related to density.

Whio only occur on the two largest islands of the New Zealand archipelago, the North and South Islands, with genetic differences between islands implying that dispersal between the two islands is highly unlikely (Robertson et al. 2007b). The relationships between whio habitat, fitness and density may by influenced by these genetic differences, potentially changing the way that managers need to prioritise sites. Therefore, I examined the quality of whio habitat in nine New Zealand rivers, assessing the relationships between fitness, occupancy and habitat between the two islands and within each island. If the fitness of whio is determined by habitat quality, then I expected whio pairs would preferentially occupy areas of good habitat, and those pairs would be in better condition, produce more offspring and occupy shorter riverine territories.

Methods

Study sites

Whio habitat was sampled from nine rivers across New Zealand (Figure 1). The rivers occurred across a broad geographic range and included a representative sample of the wide range of habitat types that whio are known to occupy (Chapter One). All rivers had been managed for whio by the New Zealand Department of Conservation using large-scale mammalian predator control for a minimum of two years. Predator control primarily targeted mustelids with linear trap lines, a technique that has been shown to significantly improve whio productivity (Whitehead et al. 2008). I restricted the collection of data to years when predator control was present to ensure the fledging rate was not constrained by predation, so that habitat-fitness relationships were likely to reflect habitat quality. Individual whio at each site were identified by unique colour band combinations,

Table 1. Habitat parameters measured for nine New Zealand rivers managed for whio conservation. Parameters were derived from an intensive field survey and the River Environments Classification (REC) geographic information system and are measured as average values over a 200 m reach.

Channel Morphology (Field survey)	**Mean and Range**
Width – mean channel width (m)	23, 5 to 70
ForDep – area of reach less than 0.6 m deep (%)	52, 0 to 100
Pfankuch – An index of river disturbance (Collier, 1992)	93, 62 to 131
LWD – area of reach with exposed large woody debris (%)	8.6, 0 to 100
ExpBou – area of reach with exposed boulders (%)	58.6, 0 to 100
UnvIsl – area of reach with exposed gravel islands (%)	4.2, 0 to 100
VegIsl –area of reach with early successional islands (%)	2.9, 0 to 100
MatIsl – area of reach with mature forest islands (%)	3.6, 0 to 100
Cascade – area of reach with cascade habitat (%)	19.1, 0 to 100
Riffle – area of reach with riffle habitat (%)	45.9, 0 to 100
Run – area of reach with run habitat (%)	19.8, 0 to 100
Pool – area of reach with pool habitat (%)	15.1, 0 to 60
Braided – area of reach with braided channels (%)	10.3, 0 to 100
Riparian cover (Field survey)	
ForDis – distance to the nearest forest cover (m)	18.1, 0 to 500
MatFor – area of riparian margin with mature forest (%)	45.6, 0 to 100
RegFor – area of riparian margin with regenerating forest (%)	9.51, 0 to 100
ExoFor – area of riparian margin with exotic forest (%)	1.31, 0 to 50
Scrub – area of riparian margin with scrub (%)	7.77, 0 to 100
Tussock – area of riparian margin with tussock (%)	1.54, 0 to 100
Grass – area of riparian margin with exotic grass (%)	9.04, 0 to 100
Heath – area of riparian margin with heath (%)	0.87, 0 to 50
Gravel – area of riparian margin with bare gravel (%)	14.8, 0 to 100
Cliff – area of riparian margin reach with cliffs (%)	9.43, 0 to 100
Local scale predictors (REC)	
SegSumT – summer air temperature (°C)	15.4, 11.5 to 18.3
SegTSeas – winter air temperature (°C), normalised with respect to *SegSumT*, i.e. $SegTSeas = \left(\left(\frac{W-\overline{W}}{\sigma_W}\right) - \left(\frac{S-\overline{S}}{\sigma_S}\right)\right) \times \sigma_S$ where W is the winter temperature for a segment, $\overline{W}$ is the average winter temperature for all segments, σ_W is the standard deviation of winter temperature, S is the summer temperature, and so on.	0.33, -0.71 to 2.01
SegLowFlow – segment mean annual 7-day low flow ($m^3\ s^{-1}$), fourth root transformed, i.e. $(\text{low flow} + 1)^{0.25}$	1.24, 1.00 to 1.82
SegFlowStability – annual low flow/annual mean flow (ratio)	0.33, 0.08 to 0.52
SegSlope – segment slope (°), square-root transformed	1.58, 1.00 to 5.68
SegShade – riparian shade (%)	0.50, 0 to 0.8

Table 1 (continued)

Landscape scale predictors (REC)	Mean and Range
USAvgT – average air temperature (°C), normalised with respect to *SegSumT*	1.95, -4.5 to 1.12
USRainDays – days per year with rainfall greater than 25 mm	53.4, 8.9 to 103.5
USSlope – average slope in the catchment (°)	24.7, 3.5 to 44.9
Landscape scale predictors (REC)	
USCalcium – average calcium concentration of underlying rocks, 1 = very low to 4 = very high	1.51, 0.77 to 3.89
USHardness – average hardness of underlying rocks, 1 = very low to 5 = very high	3.46, 2 to 5
USPhosphorus – average phosphorus concentration of underlying rocks, 1 = very low to 5 = very high	1.74, 0.77 to 3
USLake – area of lake in catchment (%)	0.003, 0 to 0.16
USNative – area with indigenous vegetation (%)	0.95, 0.61 to 1
USGlacier – area of glacier in catchment (%)	0.01, 0 to 0.22

with some birds also fitted with radio transmitters. The entire length of each site was surveyed by Department of Conservation staff a minimum of three times during each breeding season to assess the number of pairs, ducklings and juveniles, as well as territory boundaries. Some sites were monitored more intensely, but did not reveal substantial deviations from patterns established in standard monitoring, indicating accurate data on the spatial distribution and fitness of whio pairs were obtained from a large range of sites.

Habitat sampling

Annual whio territories were delineated in ArcGIS (ESRI 2008) using Department of Conservation sighting records, and were used to define the upper and lower boundaries of whio occupation on each river. Between these boundaries, rivers were divided into a series of consecutive 200 m reaches that were surveyed on foot during the 2007/2008 austral summer. Local habitat within each reach was assessed by estimating the average value of each habitat predictor across the entire 200 m (Table 1). This procedure produced a continuous measure of habitat along the river network rather than a series of point estimates that may have missed factors or reaches that were biologically important. Ad-

ditional environmental predictors were obtained from a geographic information system database (River Environments Classification; REC) developed to predict the distributions of freshwater biota (Leathwick et al. 2008), and which described characteristics of the entire New Zealand river network at a spatial resolution ecologically relevant to whio. Each stream or river section in this database is represented by a unique segment between adjacent confluences. Individual 200 m reaches were linked to a network segment in ArcGIS to obtain relevant habitat variables from the REC. It was unknown whether absences of whio within a reach were due to poor habitat quality or other biological factors such as predation or low population density, so any reaches where whio were absent during the period of monitoring by the Department of Conservation were not considered.

I decided to measure habitat at the 200 m reach scale rather than over whole territories for several reasons. Firstly, whio territory boundaries are very mobile (Williams and McKinney 1996) and display considerable movement between years. Therefore, it was not possible to define average territory areas over all monitoring years within a river. Moreover, whio are known to utilise different habitat features within a territory through-

Table 2. Fitness parameters measured for whio in nine New Zealand rivers managed for whio conservation. Data were obtained from the New Zealand Department of Conservation and are recorded as average values over a 200 m reach.

Whio fitness	**Mean and range**
Length – average length of whio territories associated with reach (km)	1.4, 0.2 to 4.0
Condition – average ratio of body weight to tarsus length for pairs occupying the reach (ratio)	18, 13.3 to 24.2
Occupancy – average number of years during monitoring period that a pair of whio occupied the reach (proportion)	0.77, 0.125 to 1.75
Per capita reproduction – average number of fledglings produced per pair per year on reach	1.45, 0 to 5
Density – average annual number of pairs per km of occupied habitat per river	1.03, 0.47 to 1.57
Reproduction per unit area – average annual number of fledglings produced per km of occupied habitat per river	1.19, 0.25 to 2.34

out the year (Collier and Wakelin 1996) and my approach provided me with information about this habitat variation at an appropriate scale.

Habitat preferences and fitness consequences

Data on whio habitat preferences and fitness were collected by Department of Conservation staff during routine monitoring over the period 2000-2008. I only include data for pairs that were observed at least three times within a season. I used whio density as an indicator of habitat preference at the broadest geographic scale. Territory occupancy was used to estimate habitat preference at the local scale and was calculated as a ratio of the number of years that a 200 m reach was within an occupied territory relative to the number of years the reach was monitored. Some reaches fell across territory boundaries and were occupied by more than one pair, giving an occupancy rate greater than one.

I used reproductive output per unit area, measured as the mean annual number of fledglings produced per km within each river, to assess whio fitness at the landscape scale. Three predictors were thought likely to be useful indicators of whio fitness at the reach scale: territory length, whio condition and fledging rate. Territory length was calculated by averaging the length of all territories that intersected with a given 200 m reach throughout the monitoring period. The Department of Conservation routinely caught family groups of whio at the end of the breeding season to band the fledglings and weigh and measure all birds. I used this information to calculate the condition of individual whio as the ratio of body weight to tarsus length (Jakob et al. 1996). Condition values were calculated annually for individual birds and an average condition score was produced for each pair within a territory. Mean pair condition scores over the whole monitoring period were assigned to individual 200 m reaches. I also calculated the mean number of fledglings produced per pair annually (per capita reproduction) over the monitoring period, and these values were assigned to individual 200 m reaches.

Statistical modelling

Patterns of habitat use were examined in relation to fitness between the North and South Islands, and between rivers within each island (Figure 2). Hereafter, these analyses are referred to as between-island and within-island, respectively.

To evaluate potential differences in habitat quality between islands, I pooled data from 200 m reaches to the level of rivers. I assessed the relationship between whio density and reproductive output per pair and per km at the between-island scale to determine whether whio density can be used as an indicator of habitat quality.

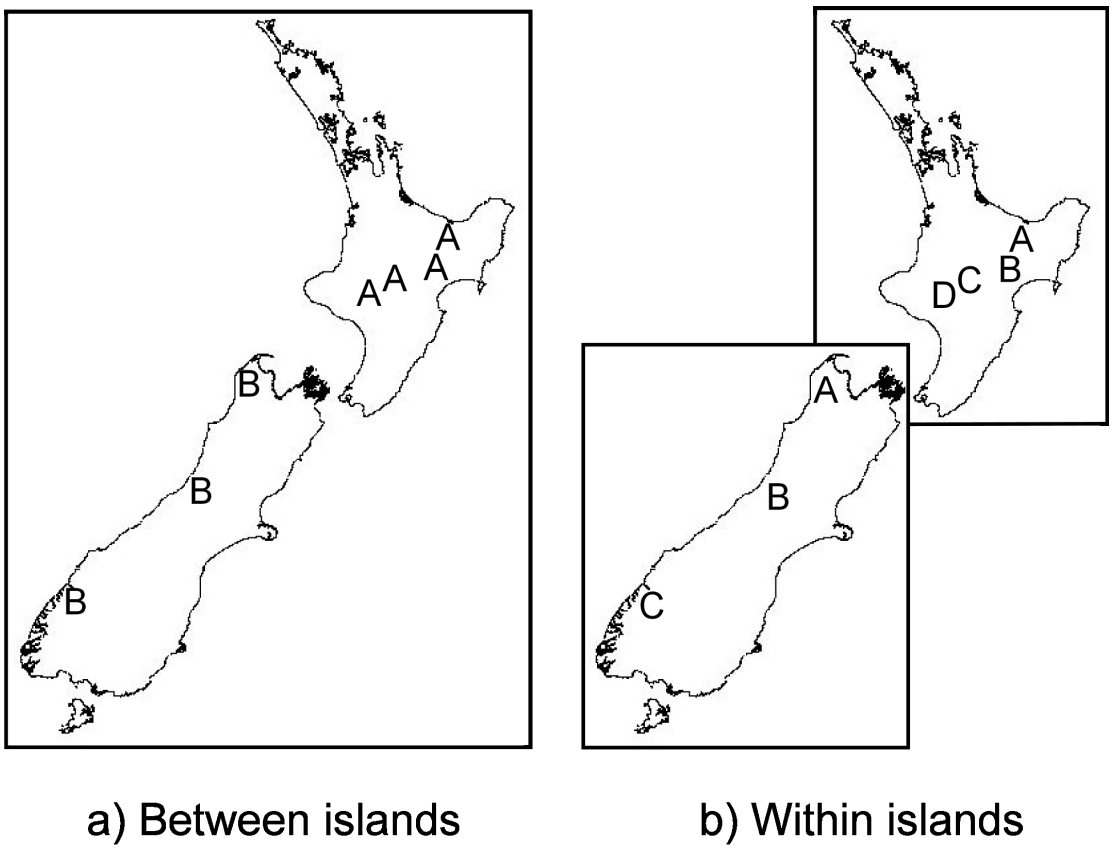

Figure 2. The hierarchical multi-scale approach used to determine the relationship between whio habitat and fitness at two scales. Boxes represent the overall scale at which an analysis was conducted, while letters indicate rivers that were treated as replicates for an analysis. The between-island analysis (a) used pooled data for each river and compared rivers between the North and South Islands, whereas the within-island analysis (b) used the 200 m reach-scale data and compared rivers within islands separately.

Habitat quality was assessed by examining the relationships between occupancy, fitness and habitat at each spatial scale. Data were transformed using log or arc-sine transformations as required to meet the assumptions of normality. First I used principal components analyses (PCA) to identify the relationships between occupancy and the three measures of fitness at each spatial scale. I examined the loadings of each variable on the first orthogonal axis of the fitness PCA, retaining the axis for subsequent analysis.

The relationships between habitat characteristics at each spatial scale were examined using a second set of PC analyses. These reduced the habitat data to a small set of orthogonal variables that were used to assess the relationships between whio habitat and fitness. I included the first five axes from the habitat PCA in an additive generalised linear model with the first fitness axis as the response to identify the strongest relationship between habitat and fitness. The most parsimonious model was selected using Akaike's Information Criterion (AIC). Potential differences in habitat quality between the North and South Islands were detected by summarising the first axis of the fitness PCA and the first five axes of the habitat PCA in a similarity matrix. Then I conducted an Analysis of Similarities (ANOSIM) to test for significant differences between islands with respect to their fitness-habitat relationship.

This analysis procedure, from fitness and habitat PCAs through to ANOSIM, was repeated on separate datasets for the North and South Islands using 200 m reach-scale data to identify the characteristics of habitat quality within the each island. All analyses were conducted using R (Version 2.1.1, R Development Core Team 2005).

Results

Whio habitat was measured in 446 reaches, providing a continuous record of 89.2 km of habitat across the nine rivers. Within this habitat, I obtained measures on the fitness of whio pairs for 326 territory-years.

Overall, whio density was positively correlated with reproduction per unit area (Figure 3a; $R^2 = 0.56$, $p = 0.01$) at the between-island scale, suggesting that density is a reasonable indicator of likely whio fitness. However, there was no significant relationship between density and per capita reproduction (Figure 3b; $R^2 = 0.05$, $p = 0.52$), indicat-

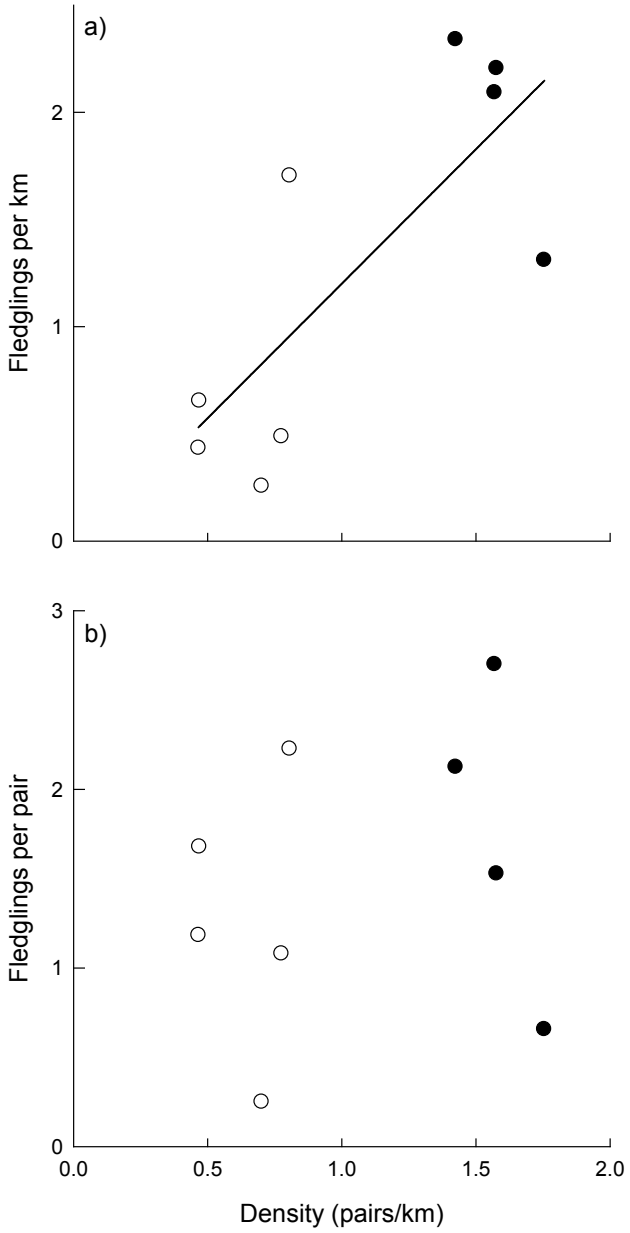

Figure 3. The effects of whio population density on (a) reproduction per unit area (fledglings per km of river; $R^2 = 0.56$, $p = 0.01$) and (b) annual per capita reproduction (fledglings per pair; $R^2 = 0.05$, $p = 0.52$) in nine New Zealand rivers (North Island, black; South Island, white).

ing there were no density-dependent effects on fledgling production at current population densities.

The first axis of the PCA, which examined the relationship between occupancy and the three measures of fitness at the between-island scale revealed per capita reproduction increased with increasing occupancy but decreased with territory length. This axis explained 53 % of the variation in fitness and was strongly correlated with axis one of the habitat PCA (Figure 4; $R^2 = 0.62$, $p = 0.012$). Axis one of the habitat PCA explained 30 % of the variation in habitat and represented a climatic and geological gradient. This meant that whio in habitats characterised by relatively warmer year-round temperatures,

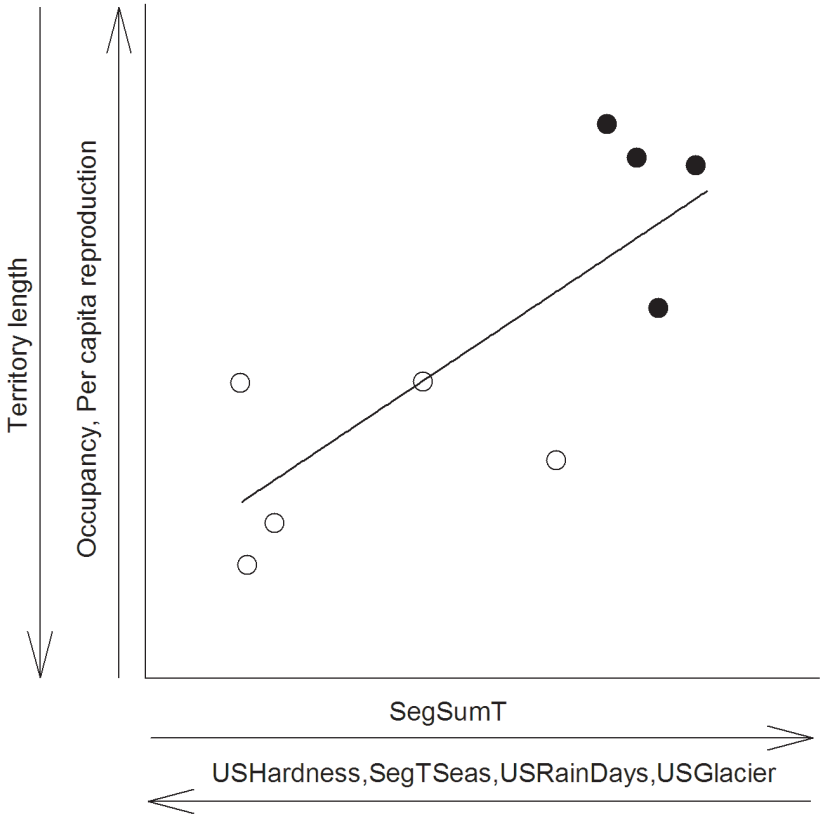

Figure 4. **The most significant relationship between whio fitness and habitat for nine New Zealand rivers** ($R^2 = 0.62$, $p = 0.012$; North Island, black; South Island, white). The plot is derived from axes based on separate PCA ordinations for habitat and fitness, with points representing mean values for individual rivers. Axes are scaled in ordination space, with arrows representing the direction of habitat and fitness gradients. Definitions of axis labels are given in Tables 1 & 2.

low annual rainfall and softer upstream geology, preferentially occupied shorter territories and produced more offspring per pair. Whio fitness varied significantly with habitat at the island level, with higher quality habitat occurring in the North Island (ANOSIM: R = 0.93, $p = 0.008$).

Fitness relationships of whio varied between islands when compared at the within-island scale. The fitness of whio on the North Island was best described by a positive

Table 3. Habitat predictors that correlate with whio fitness at two spatial scales; between the North and South Islands of New Zealand and within each of these islands. Columns within a scale represent the axes of a principal components analysis of habitat predictors that significantly correlate with whio fitness. Plus symbols represent a positive association of an individual predictor with a given axis, while minus symbols represent a negative relationship. Explanations of predictor variables are given in Table 1.

	Between Islands	**Within Islands**				
		North Island			**South Island**	
PCA Axis	1	1	2	3	1	2
Variation explained (%)	29.4	46.2	10.2	5.6	37.6	5.6
Strength of fitness relationship (*p*)	0.012	$2e^{-16}$	0.011	0.012	$1.6e^{-6}$	0.002
ForDep				+		
Pfankuch			+			+
LWD			-			+
UnvIsl				+		
VegIsl				+		
Cascade				-		-
Run						+
Braided				+		
ForDis			+			
MatFor			-			
SegSumT	+				+	
SegTSeas	-	+			-	
SegLowFlow						-
SegFlowStability		+				
SegSlope				-		
SegShade		-				
USRainDays	-		+		-	
USSlope		-			-	
USCalcium		-				-
USHardness	-	+			-	
USPhosphorus					+	
USGlacier	-					

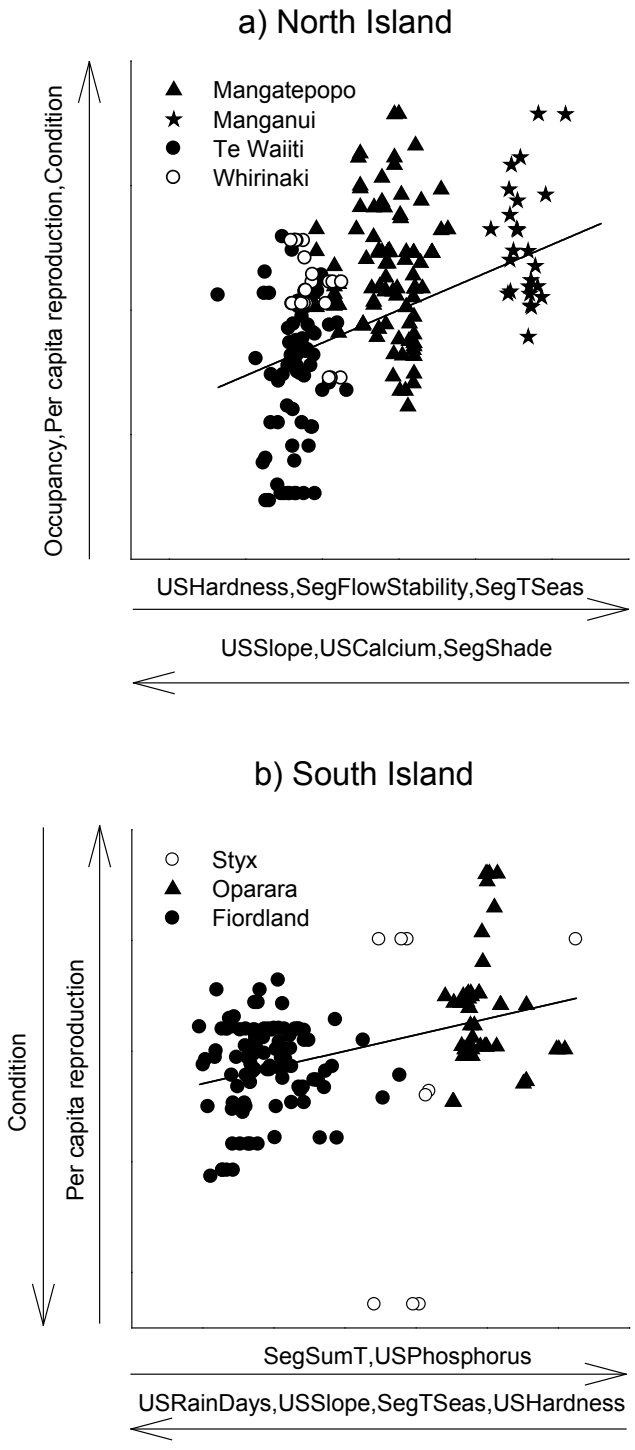

Figure 5. The most significant relationships between whio habitat and fitness measured between rivers within the North and the South Island of New Zealand. Each point represents the habitat and fitness components of an individual 200 m reach. Each plot depicts the strongest habitat/ fitness relationship for (a) North Island ($R^2 = 0.38$, $p < 0.001$) and (b) South Island ($R^2 = 0.13$, $p < 0.001$), derived from axes based on separate PCA ordinations for habitat and fitness. Axes are scaled in ordination space, with arrows representing the direction of habitat and fitness gradients.

relationship between occupancy, condition and per capita reproduction (46 % of variation explained). In contrast, condition of whio on the South Island was negatively related to per capita reproduction (38 % of variation explained).

Differences in fitness-habitat relationships were also found at the within-island scale. The fitness of North Island birds was significantly related to axes one, three and five of the habitat PCA (Table 3). Together these axes explained 45 % of the variation in habitat. Fitness was most strongly correlated with axis one of the habitat PCA (Figure 5a; $R^2 = 0.38$, $p < 0.001$), with occupancy, condition and per capita reproduction highest in habitats with stable flow, moderate seasonal temperatures, low levels of riparian shading and low gradient upstream catchments characterised by hard geology. These habitats were also shallow, low gradient streams in areas of high rainfall. Overall, there were significant differences in habitat quality between rivers within the North Island (ANOSIM: R = 0.68, $p = 0.001$), although pairwise comparisons indicated the Maunganui-a-te-ao and Mangatepopo Rivers did not differ in habitat quality (R = 0.04, $p = 0.15$).

The fitness of South Island whio was significantly correlated with axes one and five of the habitat PCA, which together described 30 % of the variation in habitat (Table 3). Fitness was most strongly correlated with axis one of the habitat PCA (Figure 5b; $R^2 = 0.13$, $p < 0.001$), with high per capita reproduction and low condition scores occurring in habitats that had warm, seasonally stable temperature and low rainfall in low gradient upstream catchments. High productivity sites were also characterised by small, disturbed stream flows with a high percentage of large woody debris. Habitat quality differed significantly between rivers within the South Island (ANOSIM: R = 0.81, $p = 0.001$).

Discussion

Animals should attempt to maximise energetic gains from foraging, while minimising the costs associated with locating food, defending territories and breeding (Fretwell and Lu-

cas 1970, Pyke et al. 1977). Therefore, if fitness is driven by habitat quality, individuals that live in high quality habitat should preferentially occupy small territories, be in good condition and have a high reproductive output. In addition, high quality habitats should be able to support a higher density of individuals (Bock and Jones 2004). However, measures of fitness, such reproduction, survival, condition and abundance, may vary in response to habitat features, leading to fitness tradeoffs and potentially providing misleading indicators of habitat quality (Johnson 2007, Kristan 2007). Non-ideal or maladaptive habitat selection can occur when there is a mismatch between habitat preference and fitness (Arlt and Pärt 2007, Pärt et al. 2007) and could potentially have serious consequences for conservation efforts. Overall, I found that high density populations of whio were most productive, as indicated by a greater number of fledglings produced per unit area. A similar relationship has been found for many bird species (Bock and Jones 2004), and suggests that whio do not occupy an ecological trap. Consequently, pair density appears to be an appropriate indicator of whio habitat quality.

Body condition may be a useful gauge of individual fitness but can be difficult to interpret as it may be an indicator of past events, an investment in future reproduction or an insurance against starvation (Witter and Cuthill 1993). I observed differences in condition between the two islands, with South Island whio in "better" condition than North Island whio. Interestingly, there was also a difference in the direction of the relationship between condition and per capita reproduction. Body condition in the South Island declined with increasing per capita reproduction and showed a strong latitudinal gradient with "better" condition whio occurring in the southernmost rivers. In contrast, the condition of whio in the North Island was positively correlated with per capita reproduction.

There are several reasons why southern whio may have a higher body condition index. The southern-most rivers experience considerably colder winter temperatures than the other monitored rivers, with whio potentially requiring larger fat reserves to survive the harsh winter temperatures. South Island whio are also skeletally larger than whio in the North Island (A. Whitehead, unpublished data), so likely require significantly more

food resources to achieve a higher condition index. Such factors will likely influence their potential reproductive output, with larger whio known to have a higher daily energy expenditure (Godfrey et al. 2003), reducing the amount of energy available for reproductive growth. For example, high energy demands may explain why South Island whio have a smaller average clutch size than whio in the North Island (Williams 1991, Whitehead et al. 2008), which in turn will limit the potential productivity of southern habitats. Conversely, this lower rate of per capita reproduction in southern whio may mean that they are in better condition because energy has been used for somatic growth instead of reproduction. If condition is particularly important for the survival of southern whio, then a high condition index is likely to maximise their fitness.

It is difficult to tease apart the mechanisms behind the observed relationships between whio fitness and habitat, but my analysis highlights the importance of using more than one measure of fitness to assess habitat quality (Pidgeon et al. 2006, Chalfoun and Martin 2007, Moyes et al. 2009). In particular, stratifying the analysis spatially allowed us to identify population differences in the relationships between fitness measures that may have important implications for conservation management. The observed patterns may be linked to differences in life history strategies between populations that enable individuals to maximise their overall lifetime fitness (Moyes et al. 2009).

Habitat quality is likely to vary over large spatial scales and consideration of the spatial structuring of populations is important for effective conservation management. The most productive populations of whio were concentrated in the North Island, where riverine habitats were characterised by warm temperatures, low rainfall and low gradient. While this pattern may suggest conservation efforts should be concentrated in the more productive North Island rivers, there may be other factors operating at this broad geographic scale that influence whio productivity. The observed habitat gradient is strongly associated with latitudinal changes in landscape-scale habitat within New Zealand, and is unlikely to reflect the cues that whio use to select habitat at a local scale. In addition, there are distinct genetic and morphological differences between North and South Island

whio (Godfrey et al. 2003, Robertson et al. 2007b), which may affect individual fitness. Such factors may mean North Island whio are inherently more productive than those in the South Island, thereby potentially increasing population growth rates. If the observed differences in productivity between islands are the result of genetic differences and not habitat quality, then the most appropriate management strategy would be to manage the two groups of whio separately (Robertson et al. 2007b).

Analyses of habitat quality within islands showed significant differences among rivers. The habitat quality gradients for both islands were determined by a combination of landscape- and local-scale parameters, with a strong latitudinal gradient apparent in the South Island. The latitudinal gradient was mirrored by the fitness measures, with higher productivity occurring in northern rivers of the South Island that were characterised by warmer temperatures, low rainfall and more stable stream flows. It may also be a reflection of genetic differences linked with an "isolation by distance" pattern of genetic similarity observed in the South Island (Robertson et al. 2007b).

Ecological traps, where the environmental cues do not reflect habitat quality, are often associated with areas of human-modified habitat (Bock and Jones 2004). However, the two most productive populations in the North Island occurred in rivers with a high degree of human modification. The section of river occupied by whio on the Manganui-a-te-ao River flows predominantly through grazed pastoral land, with some exotic and native riparian trees. The Mangatepopo River is largely surrounded by an exotic pine plantation, with regenerating native scrub and exotic species dominating the riparian margin. In addition, there is a small dam on the Mangatepopo River above the study site, where water is diverted for hydro-electricity generation. Compared with the other North Island sites, these two modified rivers had more stable water flows that may result in greater food resources (Death and Winterbourn 1995) or fewer failures of nests due to flood mitigation. Although the modified flows seemed to benefit whio, I do not advocate flow modification as a conservation technique for whio. Rather, my analysis highlights

the potential importance of modified habitats in the conservation management of threatened species (Stout et al. 2006).

Implications for whio conservation

Measures of habitat quality can help guide the prioritisation of management sites by informing managers about the most appropriate areas for conservation. However, habitat quality should be assessed at a range of relevant scales using multiple predictors of fitness (Whittingham et al. 2006, Chalfoun and Martin 2007, Johnson 2007). At a national level, current whio management is currently concentrated within eight priority sites, with the goal of securing populations of at least 50 pairs within each site (van Klink 2009). Variations in habitat quality between sites may result in spatial and temporal differences in conservation outcomes. The higher productivity of populations in the North Island means they are likely to reach target population sizes in a shorter time frame than South Island sites. In addition, North Island populations occur at much higher densities, meaning that smaller areas of contiguous habitat may need to be managed to secure these populations. My estimates of habitat quality could also be used to identify areas of habitat suitable for establishing new populations through translocation. These factors could allow valuable resources to be reallocated for protecting additional existing populations. In addition, my estimates of habitat quality could identify suitable habitats for establishing new populations through translocations of wild or captive-raised juveniles. I echo Robertson et al.'s (2007b) conclusions, recommending that management sites should be prioritised separately within each island.

Within islands, priority sites for additional management may be more effective if concentrated in warm, stable habitats but should also take into consideration the practicalities of management. Maintaining a wide latitudinal spread of sites is advisable to maintain genetic diversity, particularly in the South Island, and reduce the risk of catastrophic events extirpating populations. However, managers should avoid long distance translocations within islands to supplement existing populations or establish new ones.

For example, a large Fiordland bird may not be able to meet its energy requirements in a northern South Island river. Considering these issues of habitat quality in conservation decision making will help ensure that managers get the most ducks for their bucks.

General implications for conservation

Identifying the characteristics of high quality habitat should be an important part of any conservation strategy, as managing populations in such habitats should be more effective and greatly improve the chances of a successful outcome. The potential presence of ecological traps makes this challenging, however, and may lead to poor management decisions if unidentified (Battin 2004). Thus, it is important to correctly assess the relationships between occupancy, fitness and habitat (Battin 2004, Johnson 2007). My analyses revealed differences in the relationships between fitness measures of populations at different spatial scales that will likely alter the way populations respond to conservation management. They also highlight the importance of considering multiple measures of fitness at scales relevant to the management of population fitness, rather than individual fitness.

Acknowledgements

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Chapter Five

Tools for managing threatened species: improving the effectiveness of whio conservation

Conservation management, like emergency medicine, involves making difficult decisions about the allocation of scarce resources wisely to preserve valuable life (Bottrill et al. 2008, 2009). Managers are frequently required to make immediate responses to prevent further declines of imperilled populations, often in the absence of detailed information. In many cases, all that may be known about extant populations is their location, making it difficult to identify appropriate management strategies. If management is not targeted at the causal threat(s) in appropriate areas of habitat, then valuable resources may be wasted while populations continue to decline (Crouse et al. 1987, Beissinger and Westphal 1998, Keedwell et al. 2002). Therefore, developing a range of techniques that together can quickly and accurately identify factors that threaten species and find effective solutions is vital, particularly in these times of accelerating global change (Vitousek et al. 1997, Lee and Jetz 2008) and resource-limitation (Bottrill et al. 2009).

Effective conservation should ideally target the most appropriate management techniques in areas of high quality habitat, where organisms ought to show a faster response. A wide variety of techniques are available to identify and prioritise appropriate management strategies (i.e., Early and Thomas 2007, Arponen et al. 2008, Conroy et al. 2008, Ciarleglio et al. 2009), but all are reliant on three fundamental questions to understand the ecological effectiveness of conservation management: (1) what are the threats to population persistence, (2) how can these threats be managed, and (3) what habitats will give the greatest conservation gains? In this chapter, I develop a framework for improving the effectiveness of threatened species conservation by outlining how these three questions can be addressed using a range of demographic and spatial tools to improve the effectiveness of conservation. I illustrate my approach by summarising the analyses performed in preceding chapters to improve the effectiveness of

conservation for whio (blue duck - *Hymenolaimus malacorhynchos*), a riverine duck endemic to New Zealand that has undergone serious declines due to predation by introduced mammals and loss of forested riparian habitat. Whio have become the focus of intensive conservation management through large-scale, low-intensity predator control by the New Zealand Department of Conservation along rivers aimed at reducing mammalian predator densities within contemporary whio populations (van Klink 2009). However, prior to my research, there was little information available to guide management decisions or assess the effectiveness of whio conservation efforts.

Conservation management is often limited by a lack of information to guide decision making, reducing the effectiveness of management efforts. However, the current distribution of a threatened species can provide valuable information to inform decisions by applying a range of spatial and demographic tools (Figure 1). Species-habitat relationships derived from known ranges can identify important environmental parameters and areas of potential habitat outside the current range (Rushton et al. 2004). Such spatial information, combined with well-structured population monitoring, can identify potential threats to threatened species recovery, while demographic tools such as population viability analysis (PVA) can assess the effectiveness of management options (White 2000). Information from the spatial and demographic models will highlight areas of high quality habitat and potential relict distributions (Clout and Craig 1995, Yahnke et al. 1996). It is only by combining information from all of these sources that managers are likely to achieve the most effective conservation (i.e. utilising the best techniques in the best habitat; Figure 1).

1. Identifying historical and contemporary threats

The contemporary distribution of a threatened species represents the effects of various agents of decline that have operated within the confines of their pre-human distribution (Channell and Lomolino 2000a). Thus, effective conservation is reliant on identifying

the historical and contemporary threats that have led to the pattern of extant populations across the landscape. However, identifying threats and disentangling their relative influence can be difficult as their onset and effects are often highly correlated and may vary over large spatial and temporal scales (Gurevitch and Padilla 2004, Didham et al. 2005b, Innes et al. in press). The development of sophisticated spatial modelling techniques,

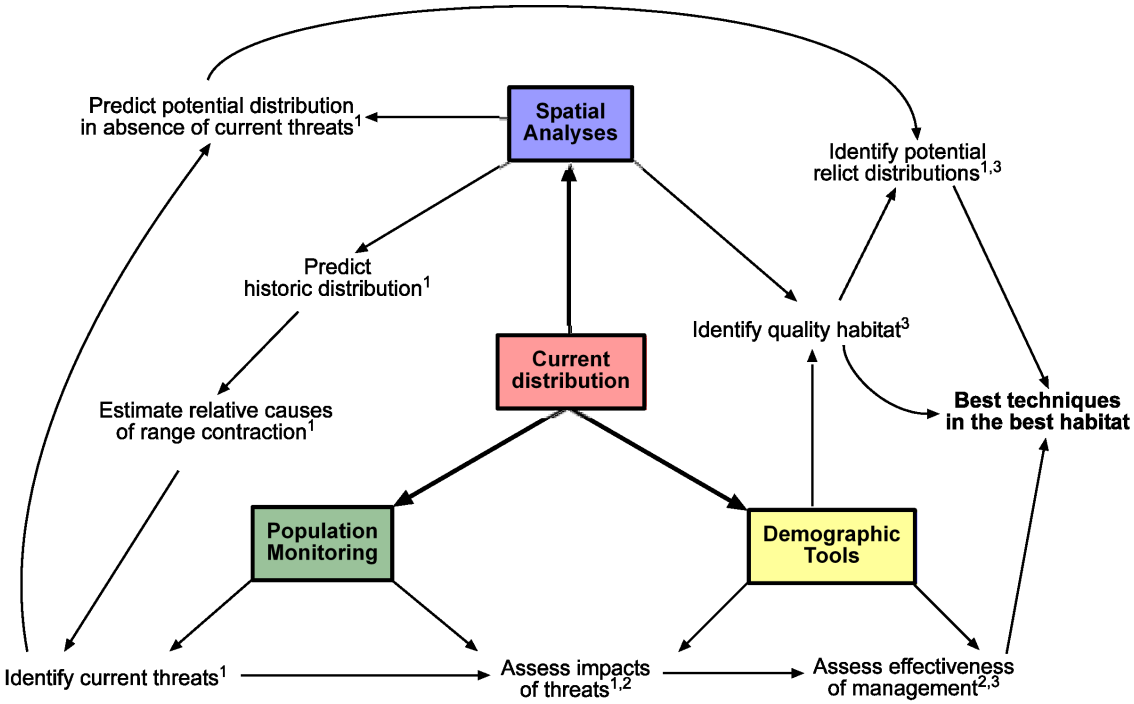

Figure 1. To effectively recover threatened species, conservation should ideally be concentrated in areas of high quality habitat, using the best available management techniques. The current distribution of a species (red) provides information that can be used in spatial models (blue) to predict the historic and potential future distributions. Differences between current and predicted historic distributions can shed light on the relative causes of historic range contraction, providing information about current threats. Well-structured monitoring programmes (green) can identify or confirm current threats and provide information for demographic tools (yellow), such as population viability analysis, that assess the relative effectiveness of alternate management options. Combining output from spatial and demographic models can identify areas of high quality habitat and highlight relict distributions, where species are confined to areas of poor quality habitat.. Only by combining information from all of these sources can managers achieve the most effective conservation. Superscripts refer to the three key conservation questions addressed by this thesis: (1) What are the threats to population persistence, (2) how can these threats be managed, and (3) what habitats will give the greatest conservation gains?

coupled with the availability of high resolution environmental data over large scales, provides a unique opportunity to assess the relative impacts of known threats on a species' range contraction (Chapter One; Eikaas and McIntosh 2006). Using the contemporary distribution to establish the extent of a species' range, it is now possible to predict the potential distribution of organisms in the contemporary environment (Guisan and Thuiller 2005), as well as predict their historical distributions by hindcasting to historical environmental conditions (Hilbert and Ostendorf 2001, Waltari and Guralnick 2009).

I undertook a spatial analysis of the extent of contemporary whio habitat (Chapter One), combining almost three decades of whio observations with 16 ecologically relevant environmental predictors using an advanced statistical modelling technique (boosted regression trees; Friedman 2002). Applying the species-habitat relationships derived from this model across the entire New Zealand river network produced a nationwide index of likely whio occurrence. This index predicted 39,000 linear km of contemporary riverine habitat currently suitable for whio occupation. Contemporary vegetation data was replaced with estimates of pre-human vegetation and riparian shading (Leathwick 2001) to predict the potential pre-human distribution of whio (54,000 linear km). New Zealand suffered severe habitat modification after human colonisation, losing two-thirds of the native forest cover by the mid 20th century (Hall and McGlone 2006), and stoats (*Mustela erminea*), the most important introduced predator of whio (Whitehead et al. 2008), were introduced and became widespread in the late 1880s (King 2005). Therefore, the 29 % reduction in suitable habitat from pre-human times to the predicted potential contemporary habitat is likely due to an interaction between habitat modification and predation by introduced mammals. Significantly, contemporary populations of whio occupy less than 7,000 km of riverine habitat, however, and just 600 km of this habitat is actively managed using predator control (Whio Recovery Group, *pers. comm.*). Habitat within the predicted potential contemporary range is largely unmodified, characterised by large tracts of native vegetation. Therefore, the effects of predators are the likely cause of this additional 82% contraction in the range of whio. This contraction represents a catastrophic

loss of habitat due to predation, with whio currently actively managed in only 1 % of their likely pre-human range.

Quantifying the relative causes of range contraction provides a valuable insight into the drivers of population declines. Such information will help managers identify appropriate threats to target, as well as highlighting areas of suitable habitat where conservation efforts could be focussed to expand populations outside their current range. For example, my research identified mammalian predators as the greatest contemporary threat for whio, indicating that a reduction in predator impacts should halt population declines. Therefore, protecting whio populations on predator-free offshore islands offers a potential conservation solution and is a technique that has been successful for a number of New Zealand's threatened species (Clout and Craig 1995, Pryde and Cocklin 1998,

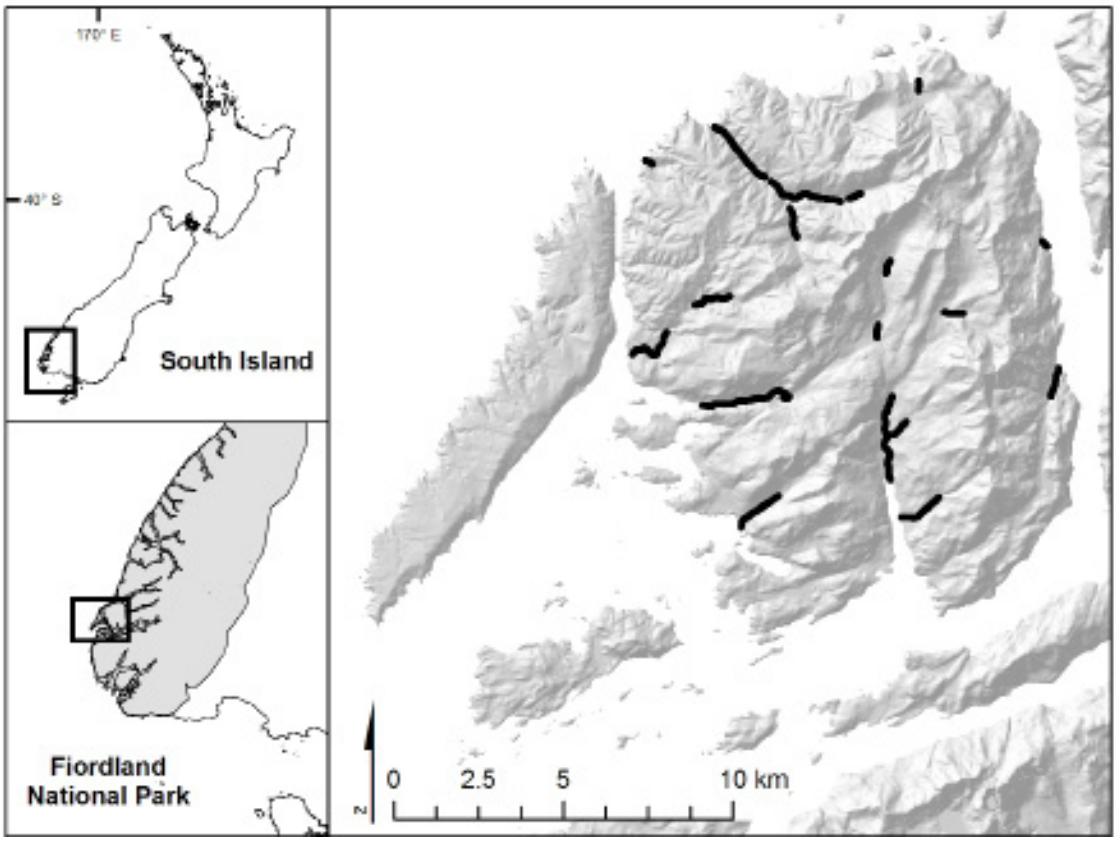

Figure 2. An example of a practical management application of the predicted likely whio occurrence index for whio. Introduced predators are currently being eradicated from 250 km^2 Resolution Island and my models suggests that this could be a potential safe haven for whio, with approximately 22 km of suitable habitat (indicated in black).

Taylor et al. 2005). To assess the potential of New Zealand's offshore islands for whio conservation, I used the contemporary index of likely whio occurrence to identify islands that contained areas of occupiable habitat. This index identified only one suitable island, Resolution Island, with approximately 22 km of potential whio habitat (Figure 2). The New Zealand Department of Conservation is currently eradicating mammalian predators from 250 km^2 Resolution Island in southern Fiordland to provide a predator-free reserve for threatened native species (Wickes and Edge 2008).

Resolution Island may provide a safe haven for a small population of whio but concentrating conservation efforts only on islands may lead to a loss of significant mainland populations and habitats. In addition, island conservation is often hampered by issues of inbreeding due to small founder populations and limited population sizes, meaning that the long-term prospects of island populations may be low (Caughley 1994, Jamieson et al. 2006). Insufficient habitat for whio on other predator-free islands indicates that an alternative method of *in situ* conservation, such as large-scale predator control in mainland habitats, is required for whio. To ensure that such predator control targets the appropriate predators, we need to clearly identify which mammalian predator(s) are linked to whio population declines.

Identifying the agent(s) of decline of a threatened species requires carefully structured monitoring of declining populations. Such monitoring should ideally be incorporated into an adaptive management framework, where an iterative process of project design, management and monitoring is used to systematically adapt and learn from previous experiences (Salafsky et al. 2002, McCarthy and Possingham 2007). Tools that allow critical life history stages to be closely monitored, such as video monitoring or radiotelemetry, can provide valuable opportunities to identify causes of mortality that may not be apparent from casual observations. In addition, such tools can help identify potential threats that may not impact the target species enough to warrant management. Current whio populations occur in relatively unmodified habitats (Chapter One, Collier et al. 1993), so mammalian predators were considered the likely cause of observed contemporary de-

clines but, prior to my research, it was unknown which species were important. Intensive monitoring of a whio population in southern New Zealand revealed that introduced stoats (*Mustela erminea*) were the primary contemporary threat to whio, with reduced nest survival and fledgling success observed in the absence of management (Whitehead et al. 2008). Clearly identifying the specific threats to whio populations allowed managers to focus conservation efforts on reducing the abundance of stoats in river catchments where whio were present, as well as providing a degree of confidence that such management efforts may be successful in reversing observed population declines.

Conservation management will only be effective if we can clearly identify the cause(s) of population declines. Long-term observational datasets are available for many threatened species, providing information for large-scale species distribution modelling to assess the relative impacts of potential threats. Combining this technique with a well-structured monitoring programme at the scale of populations can inform managers about specific threats. Together, these tools will provide information to guide the direction of management decisions and ultimately lead to an improvement in conservation effectiveness.

2. Assessing the effectiveness of management

Many conservation programmes require reliable, low-cost management techniques that can be applied over large areas to mitigate the effects of contemporary threats. For example, my spatial models predict there is currently over 39,000 km of unmanaged mainland habitat suitable for whio (Chapter One). This habitat provides huge scope for expansion of their contemporary range through conservation management, if an effective method of predator control can be identified and applied. However, limited information is often available for many threatened species, making it difficult to assess the effectiveness of management (Pullin and Knight 2009). In many cases, long-term monitoring is seen as impractical, with managers assuming that the implementation of management equates to

conservation gains (Kapos et al. 2009). However, this approach will likely lead to ineffective management, with a high risk that population declines may go unnoticed, even when management is in place.

Well-structured monitoring programmes with clearly defined measures of success are vital for effective conservation (Kapos et al. 2009). These are best established under an adaptive management framework, where monitoring data are used to inform, and adjust where necessary, management decisions (Bakker and Doak 2009). The Department of Conservation used an adaptive management approach to determine if large-scale, low-intensity stoat control was sufficient to reverse observed whio population declines and ensure long-term population persistence in southern New Zealand. Intensive monitoring of trapped catchments revealed that predator control significantly increased whio productivity but there were insufficient data to make good estimates of adult survival (Whitehead et al. 2008). Although these results were encouraging, observed increases in demographic parameters due to management may provide false hope to managers if they are not actually sufficient for long-term population persistence (Whitehead et al. in press).

PVA offers a potential way of assessing the status of populations and test the relative effectiveness of management options. PVA models are flexible tools capable of modelling relatively complex systems (Heppell et al. 1994). They can also cope with sparse datasets (Heppell et al. 2000), making them ideal for assessing the effectiveness of conservation management. PVA provides the opportunity to explore the potential relative impacts of multiple management scenarios, helping managers to make more informed decisions (Coulson et al. 2001). I constructed a series of PVA models for whio to assess the effectiveness of large-scale, low-intensity stoat control. Whio populations exposed to high levels of stoat predation had low productivity (Whitehead et al. 2008) and I predicted rapid declines and localised extinctions in areas without stoat control (Whitehead et al. in press). This finding reflects the widespread whio declines observed in unmanaged whio populations over the last 25 years (Robertson et al. 2007a). While the presence of stoat control stoats significantly increased whio productivity (Whitehead et al. 2008), models

of managed populations still had a negative mean growth rate, suggesting these populations may not be secure long term (Whitehead et al. in press). This result highlights the precarious nature of whio populations and indicates further research is needed to identify management strategies that will be sufficient to ensure long-term population persistence. Low-intensity predator control is a useful management technique for short-term whio conservation, but further intervention is likely required to prevent extinctions in the long-term.

Effective conservation requires ongoing monitoring to inform and update management decisions by evaluating the status of managed populations and the effectiveness of management strategies (McCarthy and Possingham 2007, Bakker and Doak 2009). Learning through experimentation can answer key research questions about the nature of threats and the short-term response of populations to different management options. By incorporating this information into demographic tools, such as PVA, we can assess the likely long-term response of populations to management and identify alternative management strategies that may provide better results. Such scenarios can then be trialled in the field to assess their effectiveness and continue the cycle of population viability management (Bakker and Doak 2009). Combining these tools will help to ensure long-term population persistence and improve the overall effectiveness of conservation efforts.

3. Identifying areas of high quality habitat

The best intentioned conservation management is likely to be ineffective if it is undertaken in inappropriate habitat. Conversely, conducting management in areas of high quality habitat should increase the value of management efforts as individuals will make the greatest contribution to population growth (Sergio and Newton 2003). Therefore, it is important to understand what constitutes high quality habitat. Threats often restrict species to small, fragmented areas of marginal habitat and, as a result, many threatened species occupy a relict distribution, where their current range may not reflect habitat quality

(Gray and Craig 1991, Clout and Craig 1995, Yahnke et al. 1996, Watson 2002). Such relict habitat may be of low quality, resulting in poor survival rates and low productivity, further reducing a species' ability to maintain self-sustaining populations. Such issues can make the large-scale management of threatened species problematic because it is not always apparent where conservation efforts should be concentrated to maximise returns and ensure long-term persistence. Ideally, management efforts should be concentrated in areas of high quality habitat as populations in these habitats are more likely to persist due to increased survival and/or reproductive rates (Johnson 2007). This means that fewer resources may be required to reach the desired outcome, providing opportunities to reallocate resources elsewhere (Fairburn et al. 2004).

Whio currently occur in fragmented populations over a wide range of habitat types across a broad geographic area (Chapter One), making it difficult to identify priority areas for conservation. This distribution may represent that of a generalist species, where fitness is similar across a range of habitats, or a relict distribution, where populations remain in an eclectic array of habitats not representative of habitat quality. I identified the most productive habitat for whio by comparing the habitat-fitness relationships in nine rivers managed for whio conservation (Chapter Four). When analysed at the broadest scale, whio fitness was highest in the warm, low gradient rivers. However, additional analyses identified significant differences in fitness-habitat relationships between the North and South Islands of New Zealand, indicating populations within each island responded differently to habitat characteristics. This finding suggests that North and South Island whio may have different life history strategies, allowing them to maximise their overall lifetime fitness in different habitat conditions (Chapter Four, Moyes et al. 2009).

Ideal habitat selection occurs when individuals select areas of habitat that convey the greatest fitness (Fretwell and Lucas 1970). However, species occupying a relict distribution likely exhibit non-ideal habitat selection, where populations occur in poor quality habitats with low fitness potential. To assess whether whio occupy a relict distribution, I compared the relationship between whio fitness and the index of likely whio occurrence

from my initial spatial model of whio range (Chapter One). This analysis revealed that North Island whio exhibit ideal habitat selection, with a positive correlation between whio fitness and the predicted likelihood of whio occurrence (Figure 3). In comparison, the fitness of whio in the South Island declined with increasing likelihood of occurrence, suggesting a relict distribution was likely. These patterns of ideal/non-ideal habitat selection may be linked to the observed patterns of range contraction (Lomolino and Channell

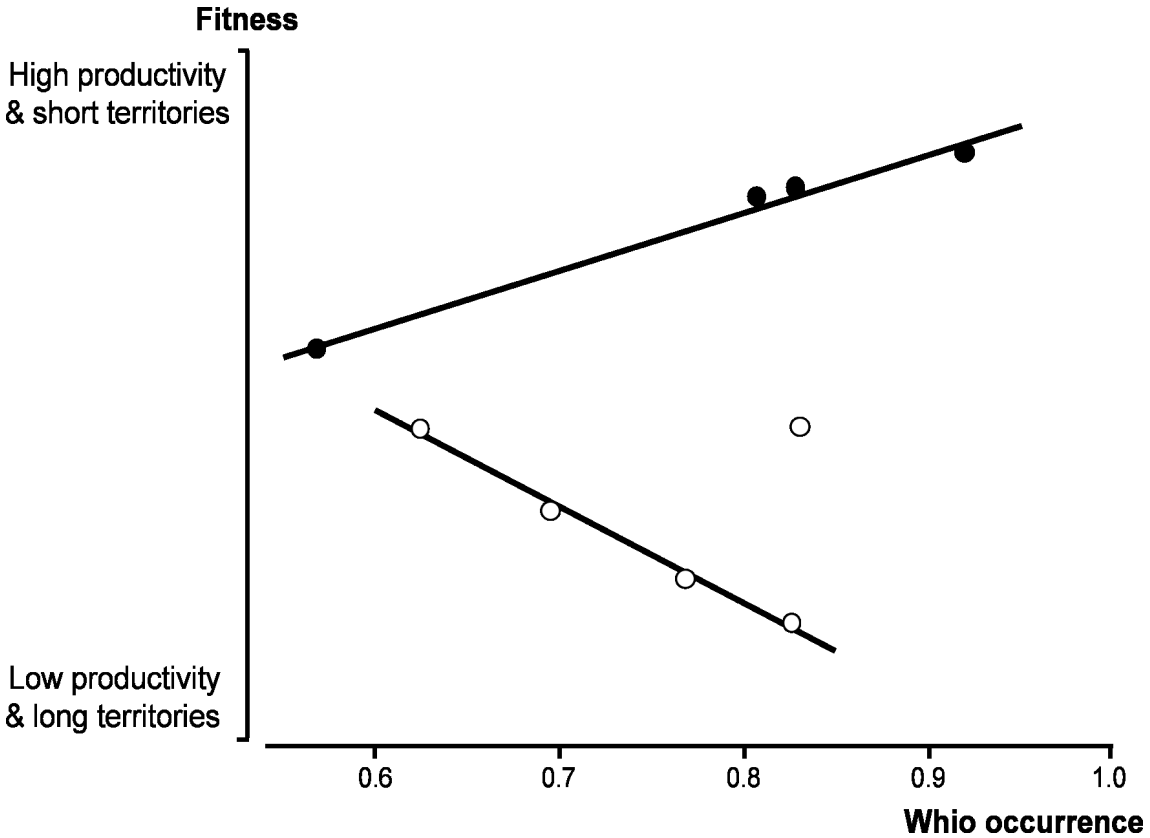

Figure 3. Spatial modelling combined with evaluations of fitness can be used to identify potential relict distributions. The fitness axis is based on a principal components axis describing increasing reproductive output and decreasing territory length (Chapter Four), while the probability of whio occurrence was predicted using contemporary distribution data in a boosted regression tree model (Chapter One). Whio in the North Island (black) of New Zealand showed a positive correlation between fitness and the predicted probability of occurrence ($R^2 = 0.99$, $p = 0.006$), suggesting ideal habitat selection. In contrast, fitness in South Island whio (white) was negatively correlated with the predicted probability of occurrence ($R^2 = 0.18$, $p = 0.47$; outlier removed - $R^2 = 0.99$, $p = 0.003$). This pattern suggests South Island whio may occupy a relict distribution, where occupied habitat is not representative of habitat quality.

1995, Channell and Lomolino 2000b). Comparisons of the predicted pre-human range of whio and their actual contemporary distribution show that North Island populations have contracted towards the centre of their pre-human range, where range contraction theory predicts that habitat quality may be higher (Channell and Lomolino 2000a). In contrast, populations of whio in the South Island have contracted into spatially isolated catchments throughout their pre-human range, with distribution likely reflecting refuges from predators rather than habitat quality *per se*. Management strategies for whio need to recognise the distinct differences in the fitness-habitat relationships between North and South Island populations and manage populations accordingly. I recommend that priority sites for management be identified separately for each island, and that translocations between sites be limited to within islands to preserve genetic diversity (Robertson et al. 2007b). Future research should evaluate the effectiveness of current management techniques in each site to assess how the quality of whio habitat affects the response of populations to management.

Developing conservation strategies for threatened species confined to a small fraction of their pre-human range can be difficult, particularly if little is known about their historical distribution or the quality of currently occupied habitat (Gray and Craig 1991, Clout and Craig 1995). However, my approach of assessing the relationship between multiple measures of fitness and habitat across a range of spatial scales can help managers identify areas of high quality habitat where conservation efforts may be more effective. Combining such information with large-scale spatial predictions of potential species occurrence can assess potential relict distributions and identify opportunities for expanding threatened species beyond their current range.

Implications for whio conservation

My framework for achieving effective conservation used population monitoring, combined with demographic and spatial tools, to identify the causes of whio population

declines and evaluate ways of improving conservation efforts (Figure 4). This research indicates contemporary whio populations have been reduced to a tiny fraction of their potential range, largely due to introduced mammalian predators (Chapter One). Nevertheless, there is considerable habitat available if the impacts of mammalian predators can be reduced. The short-term goal of the New Zealand Department of Conservation's Whio Recovery Group is to ensure the security of at least 400 pairs of whio within eight managed sites (van Klink 2009) but it is still unclear whether current management will be sufficient to meet this goal. Adaptive management and demographic models have shown

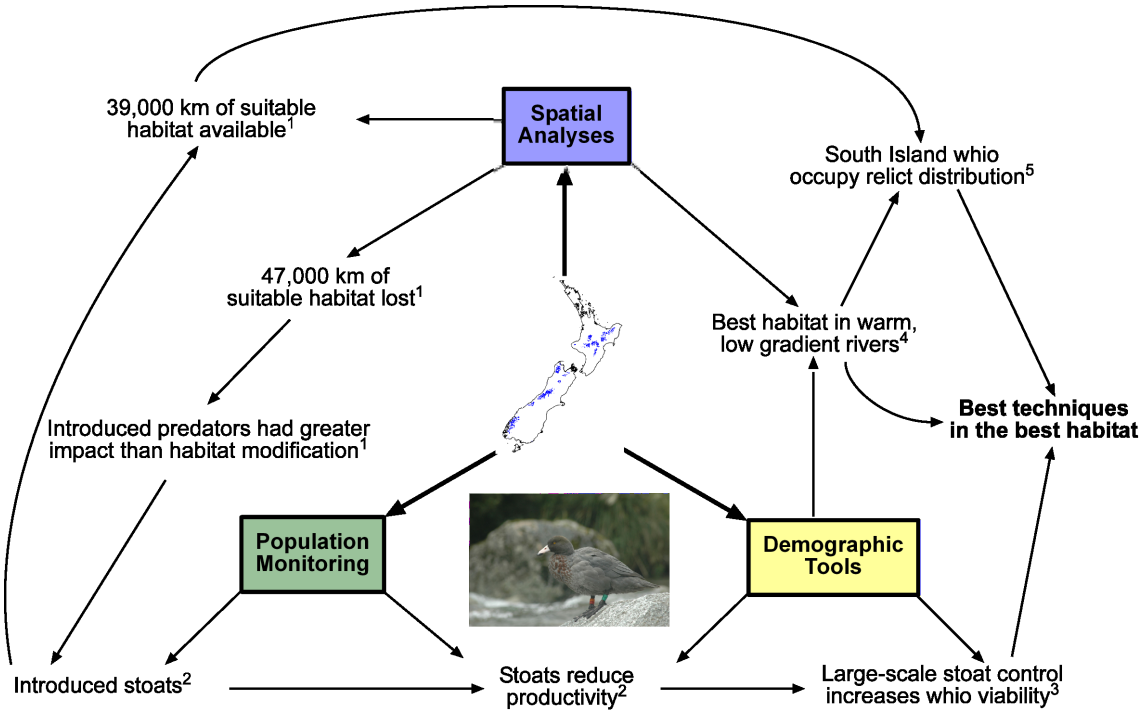

Figure 4. A combination of population monitoring, and demographic and spatial analyses has greatly increased the understanding of the conservation needs of whio (*Hymenolaimus malacorhynchos*), a threatened riverine duck. This diagram summarises the results of my research, with superscript numbers referring to the relevant chapters in this thesis. I identified an introduced mammalian predator (stoats - *Mustela erminea*) to be the primary agent of decline for whio populations. Reducing stoat numbers through large-scale, low-intensity predator control along rivers increases whio productivity but current management is not sufficient to ensure long-term population persistence. However, managing whio in areas of higher quality habitat may increase the effectiveness of conservation efforts.

large-scale, low-intensity stoat predator control increases whio population viability but further research is needed to identify strategies that will ensure long-term persistence (Whitehead et al. in press). Research should concentrate on improving understanding of adult female survival, especially in southern New Zealand, as well as assessing the effectiveness of predator control in other regions of New Zealand. Stoats were the primary agent of decline in Fiordland (Whitehead et al. 2008), but other species, such as cats (*Felis catus*) and ferrets (*Mustela furo*), have been identified as predators of whio in some areas (N. Riddler, unpublished data). It is unknown what impacts these species have on whio population persistence or how effective predator control is in reducing numbers of these predators to acceptable levels. At present, the Department of Conservation utilises a range of different predator control regimes for whio conservation (Whio Recovery Group, *pers. comm.*), from single linear traplines (Whitehead et al. 2008) to more intensive landscape control, where traplines run down both sides of the river valley and along adjacent ridges. In addition, aerial poison operations using sodium monofluoroacetate (1080), primarily to target possums (*Trichosurus vulpecula*), have been used in some areas. Anecdotally, these control regimes appear to be successful (Whio Recovery Group, *pers. comm.*) but I recommend that monitoring data from all managed whio sites be analysed using the demographic tools I have described to assess whether populations are likely to be persistent long-term. In addition, estimates of adult survival should be incorporated into the measures of fitness used in Chapter Four to provide a better understanding of quality whio habitat. Such an analysis may help to explain the potential relict distribution of whio in the South Island, providing guidance for management.

Throughout my PhD I have worked closely with the Whio Recovery Group and whio managers to develop relevant planning tools that guide management decisions. Ongoing monitoring of managed whio populations within the confines of an adaptive management approach will help to ensure that managers gain a good understanding of whio population dynamics under a range of management conditions, providing information

from which to make informed management decisions. Such a strategy will ensure that whio conservation is sufficient to provide long-term security.

General implications for conservation

My research has outlined three main challenges to the effective management of threatened species: (1) identifying historical and contemporary threats, (2) effectively managing these threats and (3) identifying high quality habitat to maximise conservation gains. Addressing all three of these challenges will provide the understanding that will ultimately improve the effectiveness of conservation management.

Conservation planning is a rapidly growing field, with a wide variety of techniques available to assist in the decision making process (e.g. Early and Thomas 2007, Moilanen 2008, Wiens et al. 2008). My approach has utilised population monitoring in conjunction with spatial and demographic tools (Figure 1) to increase the overall effectiveness of conservation management by improving the information available for decision making. I have concentrated my research on improving whio conservation but my approach is applicable to the management of many threatened species. Understanding the agents of decline and how their impacts can be mitigated is the key to any conservation programme and I recommend that such tools be used within an adaptive management framework that allows updated information from monitoring programmes to inform future decisions, further enhancing conservation outcomes (McCarthy and Possingham 2007, Bakker and Doak 2009).

My research has focussed on a single-species approach to conservation decision making but this approach is equally applicable to the conservation of multiple species. For example, Briggs (2009) outlined a method for prioritising the conservation of threatened species by grouping species into recovery groups based on their status and threats, and then identifying appropriate recovery strategies. The three components of my framework could be used to identify threats and provide information to guide effective recovery

strategies for individual species within such recovery groups or for recovery groups as a whole. Landscape analysis tools, such as boosted regression trees, can combine the distributions of multiple species with large-scale environmental datasets to identify appropriate areas for the management of recovery groups (Leathwick et al. 2008b). Meanwhile, an adaptive management approach to the conservation of such recovery groups could be used to identify the appropriate threats to manage, while assessing the effectiveness of different management techniques. Combined with an assessment of habitat quality, such techniques would provide a powerful tool for improving the effectiveness of conservation efforts directed at multiple species.

The cost-effectiveness of management strategies is an important consideration in today's economic climate, with many conservation agencies limited by funding (Bottrill et al. 2009). I did not explicitly evaluate the cost-effectiveness of management options, preferring to concentrate on improving the overall understanding of the ecological effectiveness of management options. However, assessing cost-effectiveness is an important aspect of management (Wakamiya and Roy 2009) and could be achieved by simply incorporating information about the costs of available management options in different types of habitat into my framework (i.e. Fairburn et al. 2004, Moilanen et al. 2008). This would provide managers with additional information to help guide conservation decisions.

Conserving species confined to a small proportion of their natural range can be fraught with challenges, particularly when little is known about the characteristics of high quality habitat. However, this is the reality faced by many conservation programmes. For example, takahe (*Porphyrio hochstetteri*) and kakapo (*Strigops habroptilus*), two threatened New Zealand bird species, were once widespread throughout New Zealand but are now restricted to tiny remnant populations and offshore islands (Clout and Craig 1995). Little is known about the factors that determine habitat quality within the historical range of these species, potentially limiting the long-term effectiveness of management efforts. My framework offers a way of improving conservation for such species by utilising information about historical distributions to identify potential habitats over a large

scale where conservation efforts could be focussed. Assessing the response of populations to management within these habitats will identify factors associated with high quality habitat and provide information to guide management strategies. By approaching conservation through an adaptive management framework, we can identify techniques to improve the overall effectiveness of conservation efforts, while continuing to protect existing populations. The integration of science with management is essential for long-term conservation effectiveness and my research provides a practical research framework to guide management decisions for threatened species worldwide.

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Acknowledgements

My first introduction to whio occurred when I spent two fantastic summers working for the Department of Conservation monitoring birds in Fiordland National Park. I am embarrased to admit that I had no idea what a whio looked like when I started but I quickly came to appreciate their distinctive call and quiet nature. Whio monitoring can be hard work - long hours in the rain in some of the most sandfly-infested parts of the country, constantly wet feet and heavy batteries to carry for what seemed like miles. But it can also be extremely rewarding - not many people can say they have been paid to live on the Milford Track. I thoroughly enjoyed the time I spent in Fiordland, working closely with Andrew 'Max' Smart, Chris Golding, Pete McMurtrie, Erina Loe, Chris Whyte, Kerri-Anne Edge and the lovely Tia, along with numerous others in the Te Anau office. Thanks for your enthusiasum in the field and your encouragement. May your rivers always be full of fluffy ducklings!

It was while I was working in Fiordland that I first met my supervisor, Angus McIntosh. He was taking part in a technical review of whio conservation and I was tasked with finding him a whio. We stood in the pouring rain, looking at habitat above the Chasm bridge and talked about all things whio. Little did I know that this was the beginning of a long and rewarding relationship. Thinking back, I'm surprised that I managed to maintain a conversation without gripping the handrailing in terror of Angus' flailing arms knocking me over the edge! Angus has been an inspirational supervisor, leading by example and providing a challenging but supportive environment in which to stretch my scientific wings. Thanks Angus.

My committee members, John Leathwick and Jim Briskie, have made great contributions to my PhD experience. John, in particular, has been instrumental in introducing me to a world of statistical acronyms - GAM, MARS, BRT, ROC, AUC. While this has led to many hours swearing at my computer in frustration over some piece of R code,

it has stretched my mind and made me a much stronger scientist. I have spent much time cursing misbehaving virtual ducks, but Moira Pryde and Graeme Elliot patiently navigated me through the minefields of MARK and population modelling in R and I am grateful for their help.

I moved to the University of Canterbury and joined the Freshwater Ecology Research Group in the School of Biological Sciences in 2006. Moving to a new environment can be a daunting step but I was immediately welcomed into the folds of FERG and I am extremely grateful for that. FERG has been a wonderful environment, both academically and socially and I have so many stories I could tell. Luckily for most of you, I will quickly run out of space! Thanks to my desk mate, Duncan Gray, for indulging my tendency to constantly talk in R code and answering my endless GIS questions; Rebecca Campbell and Darragh Woodford for being my other GIS go-to people; Justin Kitto for keeping me entertained during the writing phase; and Tanya Blakely, Hamish Greig and Helen Warburton for your patience with my stats questions. Michelle Greenwood, my mini-me, deserves a special mention. Michelle and I have been office mates, flatmates and good mates since I moved to Christchurch. Thanks Michelle for paving the way; for being craftitious, camera-mad and slightly crazy. Thanks to all the fergies - I've had a blast!

The students, faculty and staff of the School of Biological Sciences have provided both logistical support and a welcoming environment in which to undertake my studies. Thanks also to the members of LUUCE, the Lincoln University/University of Canterbury Ecology group, for sharing your passion for ecology.

Throughout my PhD I have had close links with the Department of Conservation and the Whio Recovery Group. This group is charged with leading the way forward for whio conservation and I have been impressed with the strong mix of science and practical conservation that the group brings to the task. Thank you for your support and encouragement. During the 2007/2008 summer, I travelled the length of New Zealand to survey the whio habitat in the core sites managed by the Deparment of Conservation. This was

a fantastic opportunity to observe whio in a wide variety of habitats and to meet some of the people who have devoted their lives to whio conservation. My work would not have been possible without the logistical support of Tim Allerby, Claude August, Alison Beath, Rufus Bristol, Abby Butler, Jim Campbell, Barry Chalmers, Dave Eastwood, Andrew Glaser, Graeme Quinn, Max Smart, Bubs Smith, Jo Tilson and Gavin Udy. Thank you for your logistical support and for access to the data that you and your teams have gathered over the years. Thank you also for letting me experience your passion for whio conservation. I am confident that the future of whio is in great hands.

I am fortunate to have been supported by a number of funding agencies throughout my PhD, for which I am very grateful. I received a Doctoral Scholarship through the University of Canterbury and a research grant from Transpower through the New Zealand National Parks Conservation Foundation. I have been able to attend a number of national and international conferences thanks to the support of the New Zealand Ecological Society, New Zealand Freshwater Sciences Society, and the Canterbury branches of New Zealand Federation of Graduate Women and Royal Society of New Zealand. These experiences have expanded my scientific horizons and allowed me to present my research to a wide scientific audience.

Thanks to my family and friends who have supported me throughout my academic career. Thanks to Hamish Carrad for being my rock (-mad old fossil) and helping keep things in perspective. My parents, John Whitehead and Sue Lake, have always had a strong interest in conservation and I inherited this from a young age. They have always offered enthusiastically encourged my scientific endeavours, even if it meant a kitchen full of dead fish, and I owe them a great deal of thanks for letting me develop into the scientist that I am today. Finally, to those who have inspired and encouraged me throughout my career, I am extremely grateful.

Amy Louise Whitehead

amylouisewhitehead@gmail.com

Profile

I am a PhD candidate in ecology with a keen interest in the conservation management of threatened species. My long involvement with practical conservation efforts in New Zealand, combined with my strong academic and teaching record, will allow me to make a valuable contribution to science-based conservation management in New Zealand.

Education

PhD in Ecology at University of Canterbury 2006 - 2009
Tools for managing threatened species: improving the effectiveness of whio conservation.

MSc in Forest Resources at University of Georgia, USA 2002 - 2004
Optimal harvest of shovelnose sturgeon in the Wabash River, Illinois.

BSc (First Class Honours) in Ecology & Zoology at University of Otago 1998 - 2001
Habitat selection in drift-feeding fish: Do giant kokopu play by the rules?

Academic achievements

MacDiarmid Young Scientist of the Year 2009
- Overall runner up
- Understanding Planet Earth category winner

New Zealand Freshwater Sciences Society Conferences
- Best conservation poster 2008
- Best conservation talk 2007
- Best student talk 2006

New Zealand Ecological Society Conferences
- Best conference poster 2008
- Best student talk (runner up) 2007

University of Canterbury Annual Biology Colloquium for Doctoral Students
- Highly commended talk 2008
- Best biodiversity talk 2006

University of Canterbury Doctoral Scholarship 2006 - 2009

University of Georgia Warnell School of Forest Resources
- Research Assistantship 2002 - 2004

Practical conservation

Department of Conservation

Whio (Blue Duck) Recovery Programme 2004 - 2008
- Advised the Whio Recovery Group on effective whio conservation techniques.
- Monitored whio in Fiordland to assess the effects of predator control.
- Handraised captive whio from eggs to wild release.

Kakapo Recovery Programme 2002 & 2005
- Monitored kakapo nesting success on Whenua Hou/Codfish Island.
- Handraised kakapo chicks from hatching to wild release.

Takahe Recovery Programme 2001 - 2002
- Handraised takahe from eggs to wild release.
- Monitored wild populations of takahe to assess population recovery.

Kaki (Black Stilt) Recovery Programme 2000 - 2001
- Monitored wild kaki nests to identify and assess the impacts of predators.

Department of Conservation Young Conservationist of the Year 1996 - 1997

Conservation Advocacy

University of Colorado Natural Resource Ecology Laboratory invited seminar 2008
Interviewed for *Hotspots*, a conservation documentary feature film 2006
Interviewed for TV3 News about the Kakapo Programme 2005
Fiordland National Park Summer Nature Programme invited seminar 2005
Television appearance in *Park Rangers,* a conservation documentary series 2002

Funding

Research Grants

New Zealand National Parks Conservation Foundation - Transpower Grant 2007
Australian Society of Fish Biology - Barry Jonassen Memorial Award 2000

Travel Awards

Royal Society of New Zealand (Canterbury Branch) Travel Award 2009
New Zealand Federation of Graduate Women (Canterbury) Travel Award 2009
New Zealand Ecological Society Student Travel Award 2006 - 2009
New Zealand Freshwater Sciences Society S.I.L 1987 Trust Travel Award 2008
New Zealand Freshwater Sciences Society Student Travel Award 2006 - 2007

Publications

Whitehead, A.L., G.P. Elliott, and A.R. McIntosh. (in press). Large scale predator control increases population viability of a rare New Zealand riverine duck. Austral Ecology.

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Teaching experience

Lecturing

University of Canterbury 100-level Ecology - Eight lecture series 2009
University of Otago 400-level Wildlife Management - Guest lecturer 2008 - 2009
University of Canterbury 400-level Conservation Biology - Guest lecturer 2008
University of Canterbury 300-level Conservation Biology - Four lecture series 2007

Demonstrating 2007 - 2008
University of Canterbury field trips and labs for Conservation Biology, Ecology, Environmental Engineering, and Physical Geography.

Professional development

University of Canterbury School of Biological Sciences
- Postgraduate Student Representatives Co-ordinator 2008
- Staff/Student Liaison Committee 2008
- Innovation ThinkTank 2008
- Teaching and Learning Committee 2008 - 2009

New Zealand Natural Sciences Journal - Editor in Chief 2007 - 2009

New Zealand Ecological Society - Conference Organising Committee 2007

Get more ducks for your bucks
How can we bring whio back to New Zealand rivers?

I was the Overall Runner Up and the Winner of the Understanding Planet Earth category in the 2009 MacDiarmid Young Scientist of the Year competition. The following essay and poster were submitted as part of my application and were targeted at a high school audience.

"Whiiiio! Whiiiio!"

A lone male whio (blue duck) whistles nervously at me as I wade across the icy river, upset that I am invading his territory. His mate has a nest on the bank and I've come to see if their eggs have hatched. Department of Conservation staff are concerned that whio numbers are declining, so we've set up video cameras on nests to see what's going on. This nest is well hidden under a fallen log and I have to get down on my hands and knees to see inside. Today I notice a pile of feathers near the entrance. Peering into the darkness, I confirm my worst fear - all that remains of the female and her eggs is a single wing and some broken eggshell! A predator has visited overnight with deadly consequences. Checking the video, I watch as a stoat runs swiftly into the nest. The female tries to fight back but ducks don't have sharp beaks or claws and she is quickly overwhelmed. The stoat drags her from the nest and then comes back for the eggs, rolling them out one at a time. The whole ordeal takes only a couple of minutes but will have long-lasting impacts on the whio population in this river. I leave the nest a little shaken and watch the male standing guard over an empty stretch of river. What does the future hold for him and the other whio on this river?

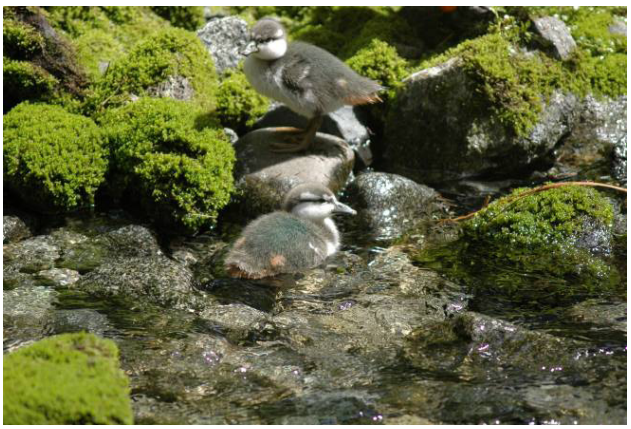
I have a strong passion for conservation in New Zealand and having witnessed the rapid decline of whio in Fiordland, I wanted to find out more about the threats that whio face and ways that we can improve their chances of surviving. These unique ducks were once common in many New Zealand rivers but their numbers have been declining rapidly in recent years due to events like the one I just described. My research uses science to answer some important questions about whio conservation: (1) what are the main predators of whio and is current management enough to protect them? (2) where could whio live if there were no predators and (3) what types of rivers are best for whio? This information will help rangers to get the most value from whio conservation, making sure that we don't lose whio from New Zealand rivers forever.

The videos indicated that stoats were the only introduced nest predators, often killing both the female duck and her eggs. Therefore, we expected that removing stoats should protect whio but would it be enough to prevent populations going extinct? Using mathematical models I found that trapping stoats led to a dramatic increase in the number of ducklings that survived, meaning that whio populations are more likely to survive long-term.

We know that current populations of whio have been reduced to a small part of their natural range because of stoats. These populations live in very different types of rivers, so I used information about these habitats to predict where they might be able to live if there were no predators. My predictions show that whio have lost over 32,000 km of river due to stoats! But this means that there is 32,000 km of additional habitat suitable for whio, if we can control stoats. This has enormous potential for whio conservation, allowing the expansion of whio populations outside their current range.

This is great news but conservation is expensive, so we need to make sure that predator control is applied in places that will benefit whio the most. To identify the best places to protect whio, I surveyed nine rivers around New Zealand and looked at which habitats produced the most ducklings. Populations with high duckling production occurred in warm, flat rivers with low rainfall. These populations will grow the fastest, meaning that protecting whio in these types of habitats will free up money for other conservation projects.

My research has shown that there is enormous potential for whio populations to expand, if we can control stoat numbers. Trapping stoats is an effective way of protecting whio and, if we can do it in the best whio habitat, we can make sure that we get the most ducks for our bucks! These tools could also help to improve conservation for other endangered species by identifying ways to increase the effectiveness of management and are a great example of how science can improve the way that we understand and manage natural systems.



Get more ducks for your bucks

How can we bring whio back to New Zealand's rivers?

Amy Whitehead
School of Biological Sciences, University of Canterbury

Whio (blue duck) are only found in New Zealand, where they live on forested mountain rivers and eat aquatic insects. There are only 2500 whio left!

- Endangered species are often restricted to small, fragmented populations due to introduced predators or habitat modification.
- However, if we don't understand these threats or how to manage them, then our conservation efforts may be ineffective.
- This is of particular concern in New Zealand where we have many endangered species but limited funding for conservation.
- I developed scientific tools to improve the effectiveness of management and increase the value of our conservation dollar.

Where could whio live?

Predators restrict many endangered species to a small part of their natural range. But we can use information about where they live now to predict where they might be able to live if we can remove these predators.

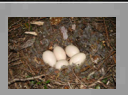
I used information about the types of habitat where whio curently live to predict where they lived in the past and could live in the future.

I predict that there is about 39,000 km of river suitable for whio, if we can control stoat numbers.

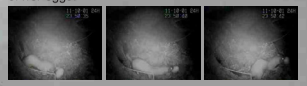
What is killing whio?

New Zealand has many unique animals endangered by introduced mammalian predators like rats and stoats. But how can we be sure that predator control is going to be enough to protect our endangered species?

DOC wanted to know what was killing whio. So we put video cameras on whio nests to identify which predators killed eggs and young ducklings.



We found that stoats are the biggest threat to whio nests. This stoat killed the mother duck and all five of her eggs!



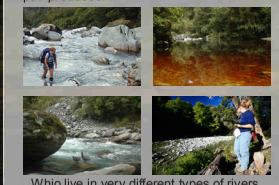
I used mathematical models to test if trapping stoats is enough to protect whio populations.

My models showed that trapping stoats increased duckling survival and led to growing populations of whio, which is great news for conservation.

Where do whio do best?

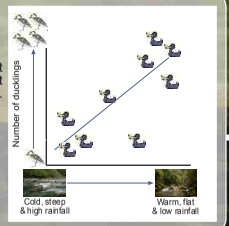
We can identify the best habitat by looking at the number of offspring animals produce. We can use this information to improve conservation by targeting management to these types of habitat.

I measured the habitat in 9 rivers where whio live and looked at how many ducklings each pair produced.



Whio live in very different types of rivers.

Whio had the most ducklings in warm, flat rivers with low rainfall.

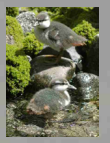


How can we get more ducks for our bucks?

Conservation is expensive, so it makes sense to use the best management techniques in the best places. Only then we will get the best value for our conservation dollars!

What have we learnt about whio conservation?

1. There is lots of habitat suitable for whio, if we can control stoats.
2. Therefore, trapping stoats in suitable whio habitat is the most effective way to protect whio.
3. My research will help managers to identify the best places for whio conservation.



My models will improve the effectiveness of conservation management for many endangered species.

My research has been supported by the Department of Conservation, Transpower, the New Zealand National Parks Conservation Foundation and the University of Canterbury. Thanks to the Freshwater Ecology Research Group & Darren Atkin from LEARNZ for design advice.